FAO Fisheries Synopsis No. 145

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SYNOPSIS OF BIOLOGICAL DATA ON THE SEAWEED GENERA Gelidium and Pterocladia (RHODOPHYTA)

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SYNOPSIS OF BIOLOGICAL DATA ON THE SEAWEED GENERA *Gelidium* AND *Pterocladia* (RHODOPHYTA)

Prepared by

Bernabe Santelices
Departamento de Biología Ambiental y de Poblaciones
Facultad de Ciencias Biológicas
P. Universidad Católica de Chile
Casilla 114-D, Santiago
Chile

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PREPARATION OF THIS SYNOPSIS

The present review concerns Gelidium and Pterocladia, the two most diversified and geographically widespread genera in the Gelidiaceae. Together they comprise over one hundred species, several of which are of common occurrence in tropical and temperate waters. Many of them are conspicuous members of intertidal and subtidal communities and locally some can become dominant because of their sizes, densities, cover or biomass values. Several species constitute food for invertebrates and fishes and a few are even consumed directly by indigenous people in different areas. Over fifty of these species are industrially or domestically used in agar production. The group is therefore biologically and economically important.

Because of the widespread distribution of several species of Gelidium and Pterocladia, quantitative and qualitative information on stocks, distributional ranges, physiological limits and utilization of these species is widely scattered in the literature. Much of this information was reviewed some years ago (Santelices, 1974). The present contribution updates that review.

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ABSTRACT

This synopsis compiles and reviews the presently available information on identity, distribution, ecology, metabolism, life history, population structure, productivity, harvest and culture, management and utilization of the genera Gelidium and Pterocladia (Rhodophyta) throughout the world.

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1. IDENTITY

1.1 Nomenclature

1.1.1 Valid scientific name

The genus Gelidium was established by Lamouroux (1813) with the European Gelidium corneum (Hudson) Lamouroux as the type species. The genus Pterocladia was first described by J. Agardh (1851) based on Fucus lucidus Turner.

1.1.2 Nomenclatural synonyms

According to De Toni (1897), the genera Clavatula Stackhouse (1801), Acrocarpus Kützing (1843) and Echinocaulon Kutzing (1843) are all synonyms of Gelidium. No specific genus is recognized as synonym of Pterocladia.

1.1.3 Vernacular names

The species of Gelidium and Pterocladia are harvested in different areas of the world and fishermen often become familiar with them. Therefore they are known in different areas under common local names. In Japan they are named "Tengusa". In Chile, both Gelidium lingulatum and G. rex are called "chasca".

1.2 Taxonomy

1.2.1 Affinities

1.2.1.1 Suprageneric

(a) Ordinal

The genera Gelidium and Pterocladia belong to the family Gelidiaceae which also includes seven other genera. The family Gelidiaceae has been considered a member both of the order Gelidiales and of the Nemalionales (= Nemaliales). The decision depends upon the acceptance of the Gelidiales as a distinct order. Life history and absence of auxiliary cells were the distinctive features used by Kylin (1923, 1928) in the original characterization of the order Gelidiales. Both characters have been critically revised thereafter.

Life history: Before 1923, the Gelidiaceae was the only family of the Nemalionales for which both tetrasporic and sexual phases were reported regularly in the literature. A "Polysiphonia type" of life history (Dixon, 1965) with an equal proportion of generations was supposed (Kylin, 1923) for the family and contrasted with the other families in the Nemalionales, which were regarded at that time as exclusively haplobiontic. This difference led Kylin (1923) to the original proposition of ordinal status for the Gelidiaceae. The occurrence of sexual and tetrasporic phases has been later confirmed in the life cycle of eight of the nine genera of the Gelidiales (Kylin, 1928, 1956; Okamura, 1934; Feldmann and Hamel, 1934; Fan, 1961; Stewart, 1968; Santelices, 1978). The exception is the genus Gelidiella where no cystocarpic thalli have yet been found. Tetrasporic thalli have been found frequently and monospores have been reported in Gelidiella refugiensis (Dawson, 1944, 1952). However, parallel to these studies, a number of authors (see reviews by Papenfuss, 1951 and Dixon, 1970) have found tetrasporic and sexual phases occurring in several genera of the Nemalionales. Therefore, one of the basic distinctions used by Kylin (1923) for separating the Gelidiales from the Nemalionales is no longer valid.

Auxiliary cell: The term auxiliary cell was first used by Schmitz (1883) to describe the hypogenous cells which fuse with the carpogonium in Naccaria. Nutrition was apparently considered by Schmitz to be the most important function of these cells, although in the majority of the Florideae it also serves (Dixon, 1959a) as the starting point for the development of the gonimoblast. The term auxiliary cell was later redefined by Kylin (1928) following his developmental studies of several red algae. Kylin distinguished cells which serve as nutritive cells from others which also constitute the starting point of the gonimoblast development. He considered the latter type of cells to be typical auxiliary cells. In these studies, Kylin examined specimens of Gelidium cartilagineum as representative of the Gelidiales, and found (Figure 1) a number of nutritive filaments developing before fertilization and closely surrounding the central cells of the procarp. The gonimoblast was described as developing directly from the unchanged fertilized carpogonium, whose growing filaments were nourished from the previously formed nutritive filaments. Thus, a typical auxiliary cell was not observed in G. cartilagineum and Kylin (1928) concluded that this was a general characteristic of the order. The only other order in the Florideae without a typical auxiliary cell is, according to Kylin, the order Nemalionales from which the Gelidiales were separated by life history differences. The absence of auxiliary cells in the Nemalionales and Gelidiales was used by Kylin as a feature separating them from the remaining Florideae.

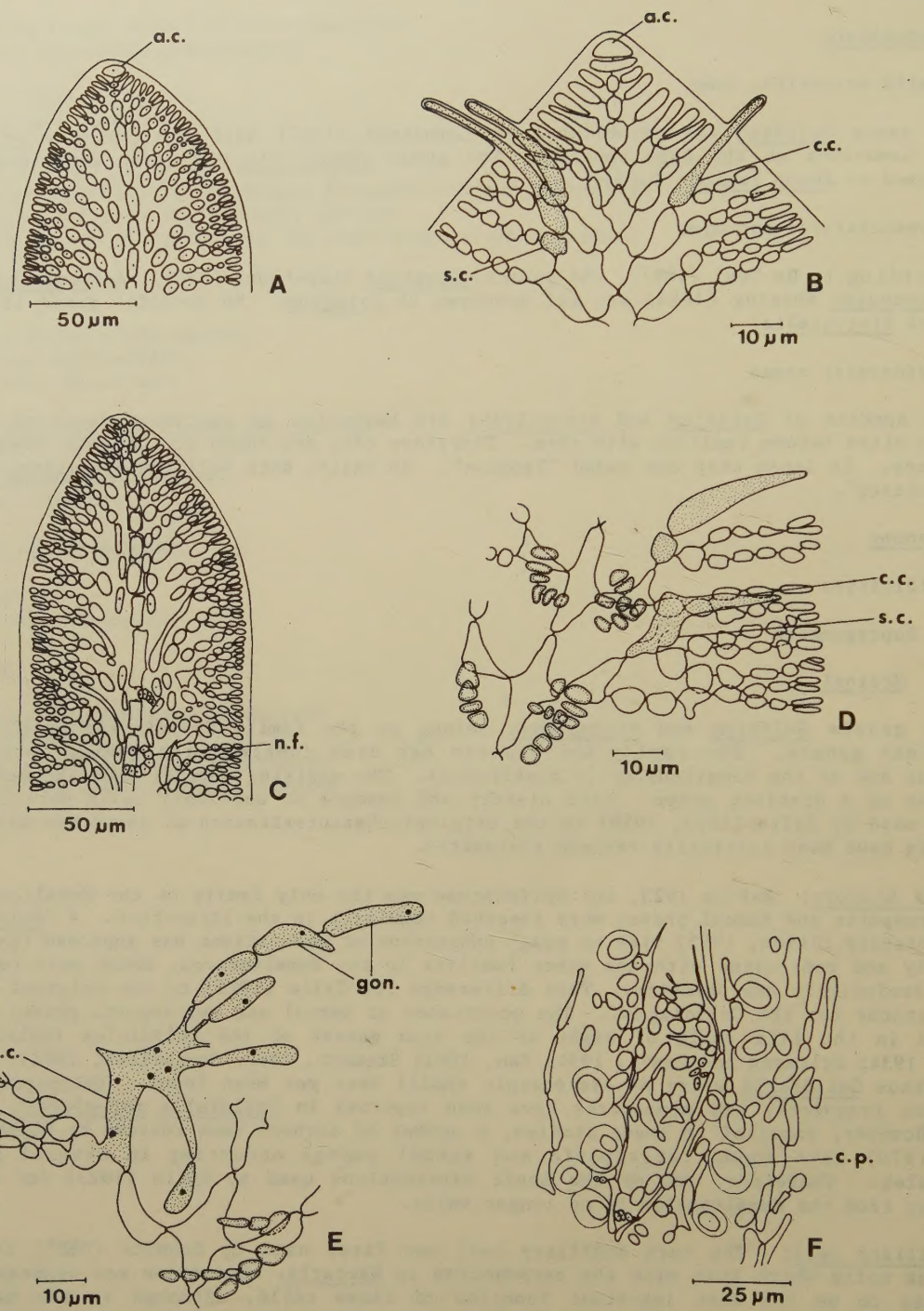

Figure 1 Morphological and reproductive classification characters in Gelidium and Pterocladia. A: Longitudinal section through the apical part of axis showing the apical cell (a.c.) and several orders of cell rows; B: Longitudinal section through a fertile ramulus showing carpogonial branches with carpogonial cells (c.c.) and supporting cells (s.c.) (after Fan, 1961); C: Longitudinal section of a fertile thallus showing nutritive filaments (n.f.) (after Kaneko, 1968); D: Longitudinal section through a fertile ramulus showing the carpogonial cell fused with the supporting cell (after Fan, 1961); E: Longitudinal section of ramulus showing fusion cells with long processes from which gonimoblast cells (gon.) have been cut off (after Fan, 1961); F: Longitudinal section through a female ramulus showing young carposporangia (c.p.) (after Kaneko, 1978)

In 1933, Svedelius reported that Asparagopsis, a member of the Nemalionales, had a typical auxiliary cell in Kylin's more limited sense. Kylin (1935) then added a further restriction to the definition of auxiliary cell: it could not be a cell in the carpogonial branch. This new restriction was strongly criticized by other phycologists. Thus, Papenfuss (1955) remarked that in Kylin's opinion, the cell or cells in the Nemalionalian carpogonial branch which receive a diploid nucleus from the fertilized carpogonium and from which the gonimoblast develops do not constitute a typical auxiliary cell; yet, Kylin himself did not hesitate in considering the supporting cell in the genus Sphaerococcus (Gigartinales) and genera in the family Kallymeniaceae (Cryptonemaliales) as having a typical auxiliary cell, even though it is a cell in the carpogonial branch system.

Since the whole classification system of the Rhodophyta is based on the characteristics of the auxiliary cell, new definitions and interpretations have been added since. Of these, one (Papenfuss, 1951) distinguishes generative from nutritive auxiliary cells. A generative auxiliary cell is practically the concept of the typical auxiliary cell sensu Kylin and applies to cells nourishing and generating or starting the generation of the gonimoblast. Nutritive auxiliary cells, on the contrary, do not serve as the starting point of the gonimoblast although they are essential to its development. They are supposed to have a nutritive function. Papenfuss stated that in the Gelidiales the gonimoblast develops from the connecting filaments following the establishment of their connection with a nutritive auxiliary cell. However, he did not mention (Dixon, 1961) the source of this information. Furthermore, the differentiation between generative and nutritional auxiliary cells does not provide (Dixon, 1961) a clear taxonomic separation between the Gelidiales and the remaining order of the Rhodophyta.

Some years later, Drew (1954) conceived the auxiliary cell as a specific cell of the gametophyte with which the carpogonium fuses before the formation of the gonimoblast, or with which the primary gonimoblast fuses. Auxiliary cells are considered to have a purely nutritive function in those cases where no nucleus is transferred. They are considered to have nutritive and generative functions in cases where the zygote nucleus or its derivative is transferred to other cells and initiates the development of a possibly secondary gonimoblast. In relation to the Gelidiales, Drew (1954) reported unpublished studies by Dixon of carpogonial development in Gelidium. The carpogonium in this genus enlarges after fertilization, and it may fuse with either the hypogenous cell or other neighbouring cells prior to any further development. However, such fusions are not obligatory, and the cell with which the carpogonium may fuse does not appear to be specifically determined. Long processes later arise from either the carpogonium or the fusion cell, and the gonimoblast develops from the tip of these processes. Work with Gelidium latifolium and G. pulchellum yielded no evidence (Dixon, 1959a, 1961) of a direct development of the gonimoblast from the carpogonium. Such direct development was previously described by Kylin (1928) for G. cartilagineum. However, Dixon (1959a) did find that the structure supposed by Kylin to represent a carpogonium and a developing gonimoblast lobe bore strong resemblance to what he interpreted as overgrown and decaying carpogonia.

Carpogonial fusions with other cells after fertilization have been also reported by Fan (1961) in the carpogonial development of four other genera in the family, namely Pterocladia, Suhria, Beckerella and Acanthopeltis. In all of them, the carpogonium enlarges after fertilization; the pit connection between it and the supporting cell gradually widens, and the two cells eventually coalesce. The gonimoblast filaments are cut off later from the tips of the processes formed by the fusion cells. Since the fusions are not obligatory and since the cells with which the carpogonium may fuse are not specifically determined, Dixon (1959a, 1961) has concluded that an auxiliary cell, in the sense in which Drew (1954) used the term, does not exist in the Gelidiales. Using the Kylin's concept of auxiliary cell and the Papenfuss' definition of generative auxiliary cell, Fan (1961) has similarly concluded that such an auxiliary cell does not exist in these species.

Parallel research in the Nemalionales has also shown (see reviews by Papenfuss, 1951 and Dixon, 1963) the occurrence of auxiliary cells in several genera. In Asparagopsis, Chaetangium and Galaxaura, the auxiliary cells are part of the carpogonial branch and therefore not typical auxiliary cells under Kylin's more restricted definition. They can, however, be regarded (Papenfuss, 1951; Dixon, 1961) as typical auxiliary cells under Papenfuss and Drew's concepts. More recent critical revisions of the classification system of the Rhodophyta (Dixon, 1961, 1970) have accepted them as auxiliary cells.

In conclusion, the important difference used by Kylin to segregate the Gelidiales and the Nemalionales from the remainder of the Florideae does not exist. Dixon (1961) has remarked that this separation can be maintained only by the acceptance of a highly suspected definition of the term auxiliary cell and proposed submerging the Gelidiales into the order Nemalionales as a single family.

Most recent treatises dealing with classification systems of the Rhodophyta (e.g., Parke and Dixon, 1964; Abbott and Hollenberg, 1976; Kraft, 1981; Bold and Wynne, 1982) have followed Dixon, recognizing the Gelidiaceae as a family in the Nemalionales. The suppression of the Gelidiales nevertheless has not gone undisputed and other criteria for separation have been advanced first by

Papenfuss (1966) and later by Pueschel and Cole (1982). The presence of nutritive cells during carpogonial development, apical growth by transverse segmentation of a single apical cell, the characteristic way spores germinate and the structure of pit plugs have all been used to further characterize the order.

Nutritive cells: As already stated, a number of nutritive filaments develop during carpogonial formation in the Gelidiaceae (Figure 1). These filaments surround the procarps and supposedly serve as a nutritional source to the developing gonimoblast filaments. The nutritive filaments have been known in the Gelidiales since Kylin's pioneer study (1928) on their development in Gelidium cartilagineum. Successive studies by Dixon (1959a) and Fan (1961) have confirmed their general occurrence in these algae.

The presence of these chains of cells has been stressed as being (Papenfuss, 1966) a striking feature of the order allowing the immediate recognition of any fertile female member of the Gelidiales. However, there are other groups of Rhodophyta which also have (Fan, 1961) morphologically similar nutritive filaments. In Atractophora and Naccaria, both members of the Nemalionales, there are (Kylin, 1928; Fan, 1961) special nutritive filaments morphologically distinguishable from vegetative filaments which are, as in the Gelidiaceae, closely associated with the carpogonial branches. In Acrosymphyton and in other members of the Dumontiaceae (order Cryptonemiales), the auxiliary cell branches are morphologically so much like the nutritive filaments of the Gelidiaceae that Fan (1961) suggested they were homologous.

Apical cell: growth in length of axes and branches, in all genera of the family, depends on the activity of dome-shaped apical cells. The apical cell cuts off segments basipetally by transverse division (Figure 1). Each such segment first divides longitudinally into one axial cell and two pericentral cells. Further divisions later increase the number of pericentral cells to four. The first two pericentral cells are formed one to the left and one to the right of the axial cell. The other two pericentral cells are produced by longitudinal divisions of the two pericentral cells and have been named (Fan, 1961) flanking cells.

The above pattern of division is apparently of general occurrence in the Gelidiaceae. It was first described by Kylin (1928) for Gelidium cartilagineum from California. Later it was found to occur (Dixon, 1958a) in Gelidium and Pterocladia from England, and finally it was observed (Fan, 1961) in the remaining genera of the order. The fact that each apical cell of the thallus cuts off only two pericentral cells has been recognized by Papenfuss (1966) as a characteristic feature of all Gelidiales.

The "Gelidium type" of germination: Using tetraspores of Pterocladia (as Gelidium) capillacea and G. latifolium var. hystrix, Killian (1914) first described the germination pattern of the order. Subsequent authors (Chemin, 1937; Feldmann, 1938; Ueda and Katada, 1949; Suto, 1950a; Katada et al., 1953; Katada, 1955; Yamasaki, 1960; Boillot, 1963; Chihara and Kamura, 1963; Kaneko, 1966; Sreenivasa Rao, 1971, 1971a; Guzmán del Proó, de la Campa de Guzmán and Pineda-Barrera, 1972; Huang, 1983; Correa, Avila and Santelices, 1985) have later described the early development of another thirteen species of Gelidium, one species of Acanthopeltis, two species of Gelidiella and one more species of Pterocladia. The tetraspores and carpospores of all the species so far studied have a similar and peculiar way of germination which has been called (Chemin, 1937; Inoh, 1948) the Gelidium type of germination (Figure 2).

Soon after the spore attaches to the substratum, a germ tube is pushed out from it. The spore contents subsequently migrate into the germ tube leaving an empty cell which is later isolated by a cross wall. By elongating and dividing, the germ tube becomes the initial cell of the sporeling. After a number of divisions, one or two rhizoids are produced from its distal end. They attach to the substratum. After a number of days, an apical cell differentiates, and subsequent thallus elongation occurs by transverse divisions of the apical cell and its derivatives.

Some cytological studies (Boillot, 1963; Kaneko, 1966; Sreenivasa Rao, 1971) have characterized the germination process in greater detail. Before the transfer of cytoplasm into the germ tube, six to eight nuclei are formed by mitotic division. When the cytoplasm moves into the germ tube, only one functional nucleus moves with it; the rest remain behind in the original spore cell where they gradually degenerate. The original empty spore cell usually disintegrates at some later stage of development. This unique ontogenetic process has been used by Papenfuss (1966) to further characterize the order Gelidiales.

Pit plugs: In a recent survey on the fine structure of pit plugs in 63 species of red algae representing 34 families, Pueschel and Cole (1982) found that the number of plug cap layers was a taxonomically reliable character when tested against other classification concepts in the Rhodophyta. They also found that members of the Acrochaetiaceae, Chaetangiaceae, Dermonemataceae, Helminthocladiaceae and Nemaliaceae, all families of the Nemalionales, have pit plugs with two-layered plug caps. By contrast, all three species of Gelidium studied (G. purpurescens, G. pusillum and G. robustum) had one plug cup layer. Consequently, Pueschel and Cole (1982) proposed the ordinal status of the Gelidiales to be resurrected.

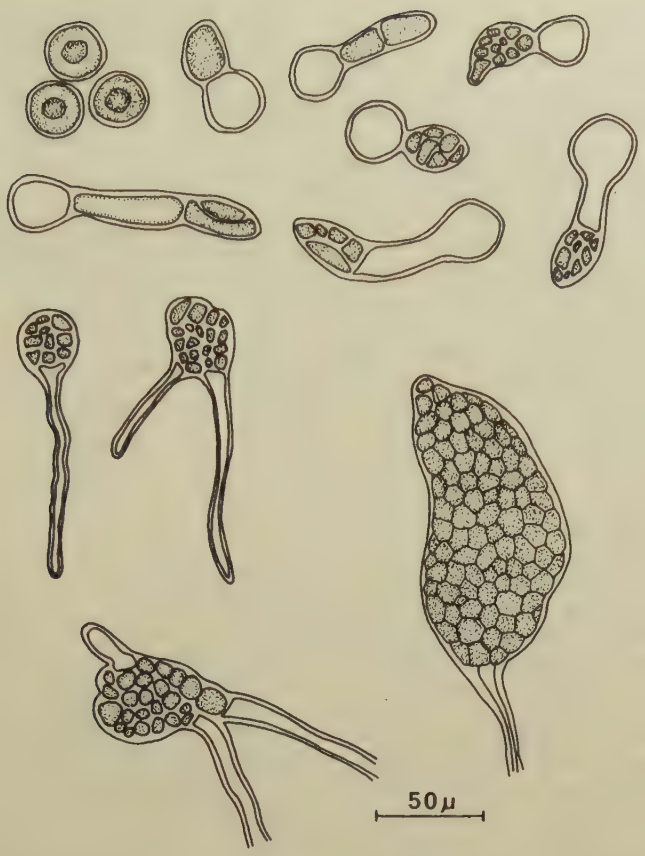

Figure 2 Early development of tetraspores and carpospores in Gelidium and Pterocladia

(b) Family

The family Gelidiaceae is closely related to the Gelidiellaceae, a family established by Fan (1961) to include Gelidioid algae lacking the internal hyphae. It includes only one genus, Gelidiella.

1.2.1.2 Generic

The eight genera presently recognized in the Gelidiaceae are Acanthopeltis, Beckerella, Gelidium, Porphyroglossum, Pterocladia, Ptilophora, Suhria and Yatabella. With the exception of Gelidium and Pterocladia, all of them can be segregated on vegetative morphological or anatomical characters (Fan, 1961). Acanthopeltis is the only genus in the family exhibiting sympodial growth. Yatabella is the only one showing multifid-echinate branches closely imbricated on the main axes. Suhria is epiphitic on Ecklonia, characterized by the absence of haptera and the presence of a disc-like basal attachment. Ptilophora and Beckerella show, in transection through the frond, a distinct inner cortical zone with large parenchymatous cells; Ptilophora has branches arising from the thallus surface while in Beckerella the branching originates from the thallus margin. Porphyroglossum is the genus morphologically closer to Gelidium and Pterocladia. However, branches and ramuli in this genus are arranged longitudinally along the median region of the fronds, with no marginal ramuli. By contrast, in Gelidium and Pterocladia the ramuli are always marginal; if ramuli exist on the thallus surface of Gelidium and Pterocladia they are irregularly arranged.

As stated previously, cystocarpic structure is the only presently accepted morphological difference distinguishing Gelidium from Pterocladia. However, due to the common scarcity of sexual thalli, this character is of limited application for routine taxonomic purposes. Five other morphological characters have been proposed to segregate these two genera, but they have not gathered general recognition. Thus, Okamura (1934) looked for differences in the hyphal distribution and concluded that in Pterocladia the rhizoidal filaments appear, densely or scattered, only in the central tissue of the thallus (medulla), whereas in Gelidium they were usually thickly congested on the external side of the central tissue (cortex). This diagnostic character was later reported to apply to species from France (Feldmann and Hamel, 1936) and Pacific North America

(Loomis, 1949, 1960). However, Dixon (1958a) found that the internal structure of British species of Gelidium changes during the life of the frond (Dixon, 1958a) and Stewart (1968) concluded that hyphae distribution patterns could change among conspecific thalli of Pterocladia capillacea in a population from California (Stewart, 1968). Therefore, this taxonomic criterion is no longer accepted as a means of segregating Gelidium from Pterocladia (Santelices, 1976a, 1977).

Simultaneously with the differences of hyphal distribution, Okamura (1934) stated that the medullary cells of Gelidium were rounded or transversely elliptical in cross section, while in Pterocladia they were more or less angular parenchyma cells and had thinner walls. If rhizoids were present, Okamura stated, the medullary cells in Gelidium would be rounded and with some intercellular spaces while in Pterocladia they were closely packed without notable intercellular spaces. Later authors, with the exception of Loomis (1949), were unable to find such differences among the medullary cells and stressed external, rather than internal, morphological differences. Stewart (1976) suggested that the lateral branches of unlimited growth of Gelidium had a basal bending at the point of branching, which was absent in the species of Pterocladia. An evaluation of this character carried out with 5 species of Pterocladia and 19 species of Gelidium (Rodriguez and Santelices, 1987a) showed that although most of the Gelidium species included in the study had basally incurved branches, some populations, for example of G. pusillum or G. japonicum, could lack the character. Likewise, while Pterocladia capillacea lacked basally incurved branches, P. bulbosa and P. caerulescens showed it. It was concluded, therefore, that the character proposed by Stewart (1976) was unreliable for generic segregation.

Based on internal morphology, Akatsuka (1970, 1981) suggested that the form, shape and disposition of superficial cortical cells might allow segregation of Gelidium and Pterocladia. Working with Japanese species, Akatsuka (1981) found that the surface cortical cells of Gelidium were ovoid, elliptical and polygonal with round corners and irregularly arranged. In Pterocladia, by contrast, the cells were ovoid, pyriform or elliptical and with their longer axis nearly parallel to the thallus axes. He also found that each oblique cell of Pterocladia had a beak-like projection on one corner near the thallus surface directed toward the thallus axes. In later studies, Akatsuka (1986, 1986a) suggested that this feature could be applied to non-Japanese species of Gelidium and Pterocladia, and used the disposition of surface cells forming pairs or tetrads for the segregation of the new genus Onisuka from Gelidium and of Pterocladiastrum from Pterocladia. Critical evaluation of the taxonomic value of this character in 19 species of Gelidium and 5 species of Pterocladia indicated (Rodriguez and Santelices, 1987a) that the character is useful when comparisons are restricted to the basal portions of erect axes. In all species of Gelidium, cortical cells close to the base were rounded and irregularly disposed. With the exception of P. bulbosa, all species of Pterocladia had the cortical cells elongated, pyriform or elliptical, with their longer axis nearly parallel to the thallus. In the case of P. bulbosa, 50% of the observations found cells similar to the Gelidium species while the other 50% reported cells similar to the Pterocladia species.

The above studies also indicated that the arrangement of external cortical cells forming pairs of tetrads suggests proportionally high rates of cell division and reduced spatial modification by cell enlargement. Several species of Gelidium and Pterocladia show this type of cellular arrangement in sub-apical portions but the feature is lost in the basalmost portions of the thallus where cell growth has disrupted the orderly cell pattern observed distally. It is not surprising then that genera of the Gelidiaceae with cortical cells arranged in tetrads along large portions of erect axes (Suhria, Porphyroglossum and some species of Gelidium) also show the presence of abundant proliferous pinnules, which probably represent increased activity of lateral initials along the erect axes. Therefore, the use of surface cells forming pairs or tetrads for the segregation of the new genera Onisuka and Pterocladiastrum (Akatsuka, 1986, 1986a) seem of doubtful taxonomic value. A better understanding of the effects that cell division and growth might have on shape and disposition of cortical cells, as well as many more data on individual and population variations of these and other characters, are required before these two new genera can be validated.

Recent studies of apical morphology revealed (Rodriguez and Santelices, 1987) intergeneric differences in the pattern of morphological organization. In Pterocladia, the axial apical initial as well as the morphologically similar lateral initials, were found strictly only in depressions between the lobes formed by the marginal projection of the outer cortical cells. In Gelidium, lateral initials have the shape of an inverted cone and are smaller than the globose, dome-shaped axial apical initials. Axial apical initials occur at the tip of axes, remaining exposed beyong the cortical cells, or in depressions between cortical lobes. Initials of lateral branches of unlimited growth occur both at depressions and at the sumit of the lobes. A critical evaluation of this character in 19 species of Gelidium and 5 species of Pterocladia indicated (Rodriguez and Santelices, 1987a) that, with the exception of P. bulbosa, it could be used to segregate Gelidium from Pterocladia. The character does not apply to Pterocladia bulbosa where the erect axes are very acute, terminating in a projecting apical cell.

Other, small-sized species of Pterocladia such as P. caloglossoides might show this apical structure as well. It should be noted however, that the whole complex of small-sized Pterocladia

and Gelidium is still taxonomically confused, and other generic and specific limits should be established for them before applying this character.

Diagnostic description of Gelidium and Pterocladia. It should be noted that the only valid morphological distinction among these two genera is the development and structure of the mature cystocarp. In both genera the thallus is cartilaginous, sometimes crispate, 2 to 40 cm tall, composed of one or several erect axes, terete or compressed, distichously, plumously or irregularly branched, red to deep purple, although in some species it can be deep green, blackish or caerulescens (Figure 3). Erect axes arise from cylindrical or compressed, branched or unbranched creeping axes with numerous short haptera extending as individual axes or forming massive disc-like holdfasts. Plants sometimes occur in mats of algal turf with extensive basal parts or in more discrete clumps. The erect fronds can be cylindrical at the base, subcylindrical above and frequently compressed at their apical ends. The margins of the axes can be entire or subentire. Often they are subentire at the basal third, irregularly sinous-dentate or erose-dentate above and variously branched along the edges of the upper half of the erect axes. The cortex has several rows of pigmented cells, the smaller usually toward the outside, mostly 2-15 µm diam., generally irregularly arranged in surface view (Figure 4).

Medullary cells are generally rounded in cross section, up to 30 µm diam., colourless, compacted or loosely appressed, with or without evident starch granules. Rhizoidal filaments are thick-walled, up to 5 µm diam., located in the medullary and/or cortical tissue, varying in number and position within species. The tetraspores in the sori occupy the entire, somewhat expanded or broadly rounded tips of lateral branches or main axes (Figure 5). Fertile branches can be simple or pinnately compound, somewhat twisted and densely congested. They often have sterile margins. Tetrasporangia are cruciately divided, up to 35 µm, and generally arranged without order in the sori. A few species (e.g., P. calaglossoides) have tetrasporangia borne in regular V-shaped rows. Spermatangial sori are sometimes apparent as relatively unpigmented areas on the apices of branchlets, usually conspicuous by the presence of a sterile darker margin. The carpogonial filament is unicellular, fusing with adjacent cells after fertilization. The morphology of the mature cystocarp is different in the two genera (Figure 6). In Gelidium, the mature cystocarp protrudes equally on both surfaces of the branch, usually with one or, more rarely, several openings on each surface of the frond. Occasionally, two cystocarpic cavities coalesce laterally, forming enlarged cystocarps of up to 1 mm long. In Pterocladia, the mature cystocarp protrudes on only one of the surfaces of the branches, usually with one or more openings on only one surface of the frond. Carposporangia are usually formed in short chains.

1.2.1.3 Specific

Gelidium and Pterocladia are the two most diversified genera of the Gelidiaceae. Gelidium comprises close to 90 species while Pterocladia includes about 15 species. Most of them however, have been described and characterized on the basis of external morphology which is quite variable within the group. In addition, many of these names are based on a few herbarium specimens barely representing the range of morphological variation of the species. All this has resulted in absence of specific limits, especially in Gelidium which appears as one of the nomenclaturally and taxonomically most confused genera of the Rhodophyta. Recent studies have related external morphological variation to environmental parameters and evaluated the usefulness of several taxonomic characters (Dixon, 1958, 1958a, 1965, 1966; Stewart, 1968, 1974; Santelices, 1976a, 1978; Santelices and Montalva, 1983). The taxonomic consequences of these studies have been a notorious reduction in the number of species distinguished in each of the geographic areas where these analyses were performed (Dixon, 1966; Stewart, 1968, 1976; Santelices, 1976a, 1977, 1987; Stewart and Norris, 1981; Santelices and Montalva, 1983; Santelices and Stewart, 1985). This sort of analysis has pointed to the need of understanding morphological variation of these species in the field before taxonomic clarification of common species of Gelidium and Pterocladia can be achieved.

1.2.1.4 Subspecies

Some authors have recognized, described and named morphological varieties in various species. In many cases these seem to correspond to ecological variants and perhaps doubtful ecotypes. These practices are likely to increase the taxonomic confusion already existing in these two genera.

1.2.2 Genetic data

Even though there can be no doubt that genetically different races may exist in the species of Gelidium and Pterocladia, we lack pertinent data, especially for those that are geographically widespread. Caryologic data are also scarce in the Gelidiaceae. The number of chromosomes in Gelidium vagum and G. amansii has been reported (Kaneko, 1966) to be seven to ten in the haploid stage. On the other hand, G. latifolium var. luxurians has been described as having a diploid number of about 30 chromosomes (Magne, 1964). The only general conclusion so far reached from these studies is that the basic chromosome number in Gelidium seems to be five (Kaneko, 1968). More data, however, are needed to evaluate whether the actual chromosome number in this and other genera of the family forms a phylogenetically meaningful series.

Figure 3 Variety of external morphologies in species of Gelidium and Pterocladia. A: G. pluma; B: G. rex; C: G. robustum; D: G. crinale; E: P. caerulescens; F: P. capillacea (A,D,E and F, after Santelices, 1977; C, after Abbott and Hollenberg, 1976; B, after Santelices and Abbott, 1985).

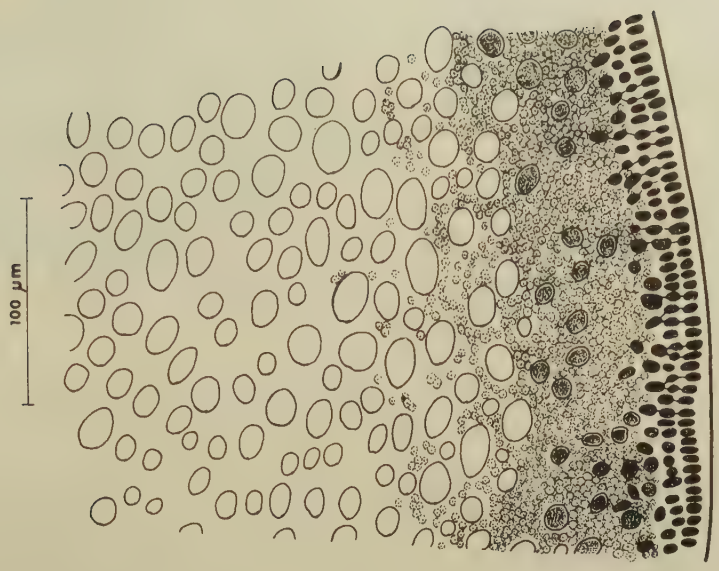

Figure 4 Transection through Gelidium showing cortical and medullary cells and the rhizoidal hyphae

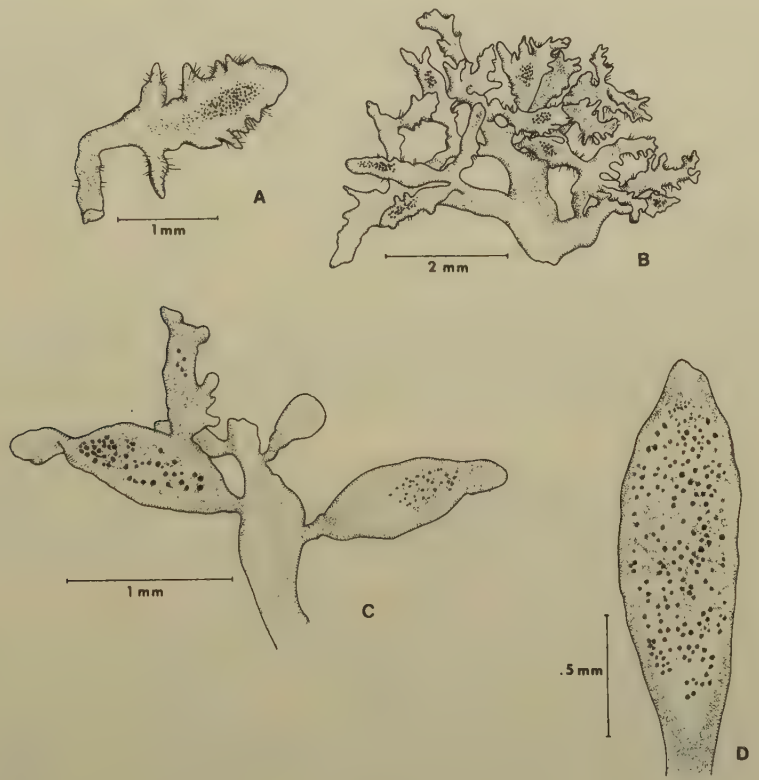

Figure 5 Examples of tetrasporangial branches in Gelidium. A and B: simple and ramified sporangial branches of G. pluma; C: soral branch of G. pusillum; D: extended sorus of G. crinale (after Santelices, 1977).

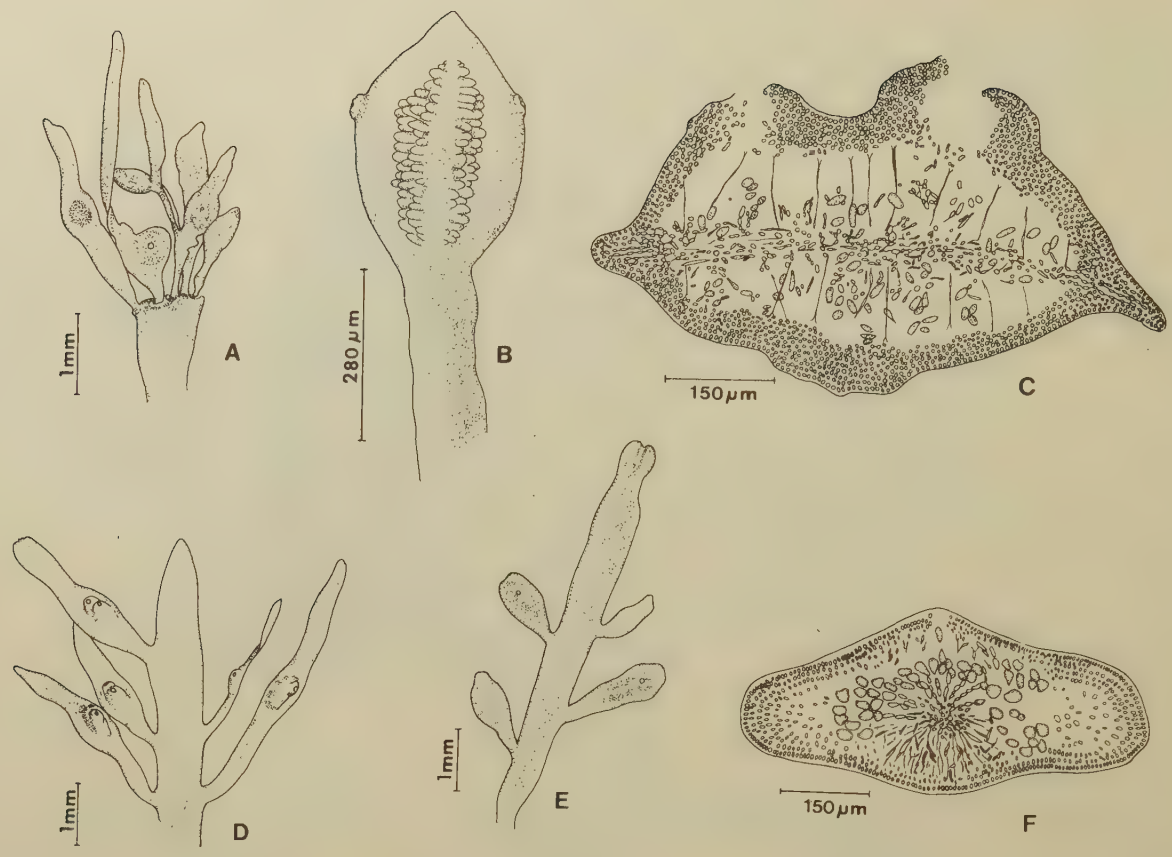

Figure 6 Morphological differences between Gelidium and Pterocladia. A and B: surface and lateral views of cystocarpic branches of G. pusillum; C: transection through a cystocarp of G. lingulatum showing bilocular cystocarps. D and E: surface view of cystocarpic branches in Pterocladia capillacea and P. caerulescens respectively; F: transection through a cystocarp of P. caerulescens showing one locule (A, B, D and E, after Santelices, 1977; C, after Santelices and Montalva, 1983; F, after Santelices, 1976).

1.3 Morphology and Anatomy

1.3.1 External morphology and variability

The plants can be small (1-2 cm) to moderately large (up to 40 cm) formed by a creeping and an erect portion (Figure 3). Creeping axes extend as separate, discrete, cylindrical axes with long haptera produced at distant intervals or with short haptera produced at irregular and closer intervals, forming a massive basal system.

The erect axes are cartilaginou, crispate and of tough consistency, terete to compressed, variously branched, red, purple, blackish or caerulescens. The erect fronds normally are cylindrical at the base, subcylindrical above, and compressed at their upper parts. They may end up in an acute or in a rounded, somewhat spathulate apex. Axes can be flat or cylindrical, entirely devoid of branches to well branched up to 4 orders. In well branched individuals, primary branches resemble main axes in external morphology and branching patterns.

The apical organization of Gelidium and Pterocladia is uniaxial (Figure 1). The segmentation of the apical cell allows the development of a primordium. The growth of the primordium commences soon after its initiation, with or without formation of lateral axes. The first stage in the development of a lateral branch is the initiation of its apical cell which arises by the transformation of a cortical cell. As a result of the segmentation of the lateral branch's apical cell, a small meristematic mound develops, growing out to form a lateral branch of unlimited growth with a structure similar to that of the main axes (Dixon, 1958). It is as yet unknown which factor determines the transformation of a cortical cell into an apical cell, but several environmental factors can probably affect this process since the branching pattern in many species is modified by the seasonally changing values of light intensity and temperature, variations in water movement and

emersion at the shore. This explains (but does not yet allow to predict) the great external morphological variability shown by many of the species of Gelidium and Pterocladia.

In recent years, there have been attempts to critically relate external morphological variations of some species of Gelidium and Pterocladia to environmental factors. Both Dixon (1958, 1963a, 1965, 1966) and Stewart (1968) suggested that external factors could not only affect the physiological activity of axial and cortical cells, but also modify the position and shape of external axes already formed, as well as the potential life span of the frond. Thus, exposure to different environmental extremes could result in different growth rates at various tidal levels, or could limit the age of the frond. Seasonal variations of light and temperature are bound to result in seasonal growth forms in several species of Gelidium and Pterocladia (Dixon, 1966; Stewart, 1968; Seoane-Camba, 1969; Gómez-Garreta, Ribera Siguan and Seoane-Camba, 1982; Echegaray-Taborga and Seoane-Camba, 1982). Reproductive periodicity could have similar effects (Santelices, 1978). Soral bleaching and apical decay after spore release in subtidal populations of Pterocladia caerulescens from Hawaii reduce thallus length and density of branches. This annual process, combined with the apparently continuous growth in breadth of main axes, results in morphologically different sterile and fertile thalli.

In most species of Gelidium and Pterocladia, spermatangial fronds are similar in external appearance to sterile branches. Therefore, without microscopic examination it is often impossible to distinguish them from other small, sterile fronds.

The sporangial branches initially look quite similar to sterile branches and in many species they remain unmodified, except for the more intense red colour resulting from the more intense pigmentation of the spores. In other species, however, fertile branches can be pinnately compound, twisted, elongated, with undulate or dentate margins, and morphologically different from sterile branchlets. Similar morphological differentiation may occur in cystocarpic branchlets.

1.3.2 Anatomy and cytology

1.3.2.1 Anatomy of tetrasporophytes and gametophytes

As stated previously, growth in length of axes and branches in tetrasporophytes and gametophytes of both genera depends on the activity of a dome-shaped apical cell (Kylin, 1928; Dixon, 1958; Fan, 1961). This apical cell cuts off a segment basipetally, by transverse division. Each such segment first divides longitudinally into one axial cell and two pericentral cells. Further divisions later increase the number of pericentral cells to four. The first two pericentral cells are formed, one to the left and one to the right of the axial cell. The other two pericentral cells are produced by longitudinal divisions of the two pericentrals; these four cells are inclined to the axis of the thallus at an angle of 30° as a result of the concave-convex shape of the segment cells. After elongation, the pericentral cell divides obliquely to form the apical cell of lateral branches of limited growth (Dixon, 1958). The oblique divisions of this apical cell continue, so that the axial filament is surrounded by cells which are at first quadrate and will constitute the medullary tissue of the axis. The divisions gradually cease and the individual cells of the final order, that is, the apical cells of the lateral branches of limited growth are those which constitute the outer layer of the cortex. Hyphae arise from the basal pole of the outer medullary cells as small protuberances, which are cut off by the formation of transverse walls, so that the cells formed are triangular, with dense contents. Rapid elongation takes place, the initials growing basipetally between the cells of the thallus and forming the hyphae. In older stages, the hyphae are thick-walled and have a narrow lumen with little cell content. Differentiation is similar in erect and creeping axes.

A transection through a mature frond of Gelidium and Pterocladia therefore shows (Figure 4) a cortex formed by several rows of pigmented cells and a medulla formed by larger, colourless cells which appear rounded in cross-section and frequently with thick cell walls. Rhyzoidal elements of up to 5 µm diameter and 200 µm length, can be abundant either in the cortex and/or in the medulla.

Sporangial sori are produced either in the terminal portions of the main axes and branches or in specialized, fertile branchlets. The sporangial mother cell is a cortical cell which is positioned terminally on a lateral cell filament (Figure 7). The mother cell enlarges and divides

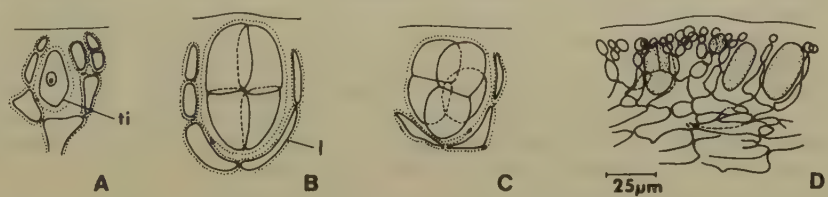

Figure 7 Tetrasporangia formation in Gelidium and Pterocladia, showing the tetrasporangia initial (ti), and the lateral cells (l). (A, B and C, after Dixon, 1959; D, after Fan, 1961)

to form four spores arranged in a cruciate or tetrahedral manner; each spore contains one nucleus (Fan, 1961). Spermatangial sori occur superficially as irregular patches on the main axis and the lateral branches (Figure 8). The superficial cortical cells enlarge, fade in colour, and become transformed into spermatangial mother cells. Each of these gives rise to two or three spermatangia, which divide transversely after their formation. It is not clear whether spermatangia are liberated from both the upper and lower cells resulting from the transverse division of the spermatangium (Dixon, 1959a). After a spermatium has been liberated from the upper cell, the lower cell appears to remain intact for some time (Dixon, 1959a).

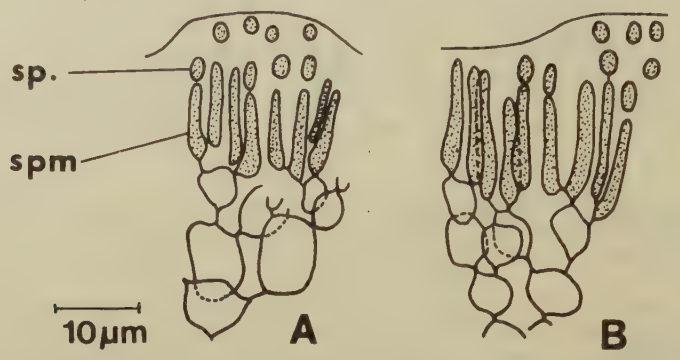

Figure 8 Spermatium formation in Gelidium (a) and Pterocladia (b)
Sp = spermatium; Spm = mother cell (after Fan, 1961)

Carpogonia are produced in the terminal parts of the main branches or on modified, fertile ramuli formed on the margins of the thallus (Figure 1). The development of a carpogonium is initiated by the formation of a lobe on a cell of a lateral branch of limited growth, normally the second basal cell of a cell-row of the third order, at a short distance behind the apical cell of an axis. The lobe elongates rapidly and it is then cut off by a wall to form a sessile carpogonium, although in some cases the wall does not develop and the carpogonium is intercalary. The carpogonium continues to elongate and the apical prolongation penetrates the surfaces of the thallus forming a trichogyne. During the development of the carpogonium, a number of conical primordia are formed from and around the cell below the one which gives rise to the carpogonium. These primordia are then cut off as small cells which divide repeatedly to form one or several rows of cells. These are recognized as nutritive cells.

1.3.2.2 Anatomy of carposporophyte

As Dixon (1959) remarked, it is not always possible to state that further development of the carpogonium is dependent upon fertilization, but the frequent occurrence of trichogynes with fused spermatia suggests that fertilization does take place.

After fertilization, the carpogonium enlarges and the pit connections between it and the supporting cell gradually widen; these two cells eventually coalesce and an irregular fusion cell is formed (Figure 1). The carpogonium then initiates one or several long, branched processes that grow toward the central axis. The tips of these processes cut off the gonimoblast initials which divide repeatedly to form the gonimoblast filaments. These filaments then form a tangled mass around the central cells of the fertile tip. Meanwhile, nutritive filaments are formed in abundance and there may be fusion between gonimoblast and nutritive cells. Gonimoblast cells later enlarge, elongate and cut off one or several carposporangia toward the surface of the ramulus. The carposporangia later enlarge greatly and elongate in the direction of the thallus surface.

In the case of Gelidium, carpogonial branches are produced on both surfaces of the ramulus. After fertilization, gonimoblast formation and carpospore production, the basal cells of vegetative filaments elongate pushing up the cortex on both surfaces of the ramulus and generating a biconvex cavity where the carposporangia develop (Figure 6). In most species of Pterocladia, carpogonial branches normally develop on only one surface. After fertilization and gonimoblast development, chains of carposporangia are cut off by some of the gonimoblast cells which are situated toward the surface of the ramulus. Formation of carposporangia and elongation of the inner wall cells to produce a cystocarpic cavity occur only on the side on which carpogonial branches are produced (Figure 6). Thus, only one locule is formed in these species. The cortical tissue on the opposite surface of the thallus usually remains compact, but at times, the surface on this side may be elevated (Fan, 1961).

1.3.2.3 Cytology

The cytology of Pterocladia capillacea has been studied by Tripodi (1971) and some observations on pit-plug structures of three species of Gelidium have been more recently made by Pueschel and Cole (1982). Cortical cells of Pterocladia capillacea show few vacuoles, the cytoplasm is rich in ribosomes, and a rough endoplasmic reticulum is visible in some parts of the cell. Mitochondria are frequent, and in general their cristae are parallel to the longer axis. Plastids are lenticular, lack pyrenoids, have the typical lamellar arrangement of Rhodophyta and contain a variable number of electron transparent areas. Large starch granules are sometimes adjacent to the external surface of the plastids, or surround the nucleus.

The internal cells of the thallus are larger than the cortical cells; they are vacuolated, with large, irregularly shaped plastids. Dictyosomes are numerous showing many vesicles with electron-transparent matrices. Often mitochondria associated with the forming face of the dictyosomes could be observed. Floridean starch granules are quite numerous in these cells. Smaller granules appeared indistinguishable from the dictyosomal vesicles while some of the larger ones could sometimes be found arranged in progressive succession with the dictyosomal vesicles (Tripodi, 1971).

The pit-connections of cortical cells of P. capillacea were first described by Tripodi (1971) as constituting a granular matrix, defined by a complex structure, formed by an internal and an external layer. In the more internal thallus cells, the pit-connections show larger dimensions, with a matrix clearly differentiated into a homogeneous internal and a peripheral part. Pueschel and Cole (1982) indicated that the pit plugs of Gelidium purpurascens, G. pusillum and G. robustum all lack a PTA-Chromic acid reactive layer on the cytopolasmic side of the cap membrane. However, a single cap layer did appear to be present adjacent to the plug core. A cap membrane, whose presence could be demonstrated most clearly by lipid extraction, was appressed to the cytoplasmic side of this single cap layer. The plug core of large pit plugs often showed striations perpendicular to the ends of the core.

2. DISTRIBUTION, ECOLOGY AND METABOLISM

2.1 Geographic Extent

When Kützing (1843) first described the family, the Gelidiaceae were characterized as a warm water group. Later studies have determined different patterns of geographic distribution for each of the eight genera presently accepted in the family but Kützing's characterization is still valid for the group as a whole. Five genera in the family, each containing one or two species, have a fairly restricted geographic distribution. Acanthopeltis and Yatabella occur only in Japan while Porphyroglossum is restricted to Java; Suhria has been found in Japan and South Africa, and Ptilophora in Australia and South Africa. Two of the other genera are restricted mainly to tropical areas, although there are specific exceptions. The genus Beckerella is represented by eight species in the Indo-Pacific and one in the Mediterranean (Okamura, 1934; Huvé, 1962; Kraft, 1976; Akatsuka and Masaki, 1983).

Gelidium and Pterocladia are the geographically most widespread genera in the family. Pterocladia includes 10-12 species (Kylin, 1965; Levring, Hoppe and Schmid, 1969) mostly restricted to tropical latitudes. Only Pterocladia capillacea and P. lucida are common in temperate waters. The genus Gelidium has any number between 50-100 species. Recent compilation of type specimens in European and American herbaria comprised over 100 names and varieties (Segi, 1963, 1977) but several of these probably are nomenclatural synonyms.

Gelidium is also the geographically most widespread genus in the family. Specific names are abundant for the tropics and less so for temperate latitudes. Species extending into cold waters are infrequent. The maximum poleward distribution for the genus is represented by G. crinale reported by Hariot (1889) from the Falkland Islands (= Malvinas) and by G. latifolium which in the Northern Hemisphere extends up to the southwest coast of Norway (Jorge, 1966; Ruesness and Tanager, 1984). Seemingly, no species of Gelidium or Pterocladia has been found in the Artic or Antartic coasts.

The present knowledge of the geographic distribution patterns of the species of Gelidium and Pterocladia is heavily dependent on taxonomic decisions. As stated previously, critical taxonomic studies considering local morphological variation and including nomenclatural analysis have been carried out only for a few species of Gelidium and Pterocladia from England, California, Hawaii and central Chile. Therefore, it does not seem meaningful at this stage of taxonomic knowledge to discuss patterns of geographic distribution for the species of Gelidium or Pterocladia.

2.2 Local Vertical and Horizontal Distribution

The vertical distribution of common intertidal and subtidal species of Gelidium and Pterocladia is summarized in Table 1. Many species occur as belts around the lower limits of spring tides extending to variable degrees into the intertidal and subtidal zones. Some of these species seem to have restricted vertical distributions (e.g., G. arbuscula in Teneriffe; G. caulacantheum in New Zealand; G. divaricatum in Japan; G. pluma in Hawaii) but many others form monocultures which can extend down to depths of 10 or 20 m. These locally abundant species often are the object of commercial fishing activities.

Very frequently, different species of Gelidium and Pterocladia occur as successive belts in a vertical elevation. This is the case of Gelidium pusillum, G. divaricatum, G. amansii, G. japonicum, G. pacificum and P. capillacea which, according to Matsuura (1958), replace each other in intertidal habitats of the Japanese coast. In Hawaii, it is possible to find G. pusillum, P. caerulescens and P. capillacea in vertical transition in exposed habitats (Santelices, 1977, 1978a). In southern Morocco and northern Mauritania, Primo (1953) described intertidal belts of G. attenuatum and G. spinulosum, replacing each other in intertidal elevation, while on the geographically close coast of Spain, G. spinolosum, G. spathulatum and G. sesquipedale show a similar trend (Fernández and Niell, 1982). On the coast of Teneriffe, P. bartletii, G. arbuscula and G. cartilagineum form successive belts (Lawson and Norton, 1971), while in central Chile, a mixed belt of G. chilense and G. lingulatum occurs between an uppermost belt of G. pusillum and a lower intertidal belt of G. rex (Montalva and Santelices, 1981).

Few studies have intended to identify the factors limiting the vertical extent of the species of Gelidium and Pterocladia, and even fewer have tried to explain the zonated pattern of ecological distribution of those species forming successive belts around the low limit of spring tides.

Desiccation has been thought to be an important factor limiting the uppermost vertical extent of some species. Thus, damaging desiccation effects were reported to occur (Chapman, 1966) in Gelidium caulacantheum, a midlittoral species from New Zealand. Five hours of exposure to atmospheres of 57 and 65% relative humidity resulted in a water loss of 35% in the shade and 50% under sunny conditions. Since relative humidity in the field is somewhat higher, the probable loss of water content during the 9 hours of estimated average of intertidal exposure was calculated to amount to (Chapman, 1966) 50 percent. Photosynthesis continued, depending on relative humidity, up to a maximum limit of 8 hours, the rate being strongly affected by desiccation. Therefore, Chapman (1966) concluded that the upper limit of this species is probably determined by water loss during emersion and its subsequent effects on photosynthesis and respiration. Likewise, extreme dehydration reduced the respiration rates of Gelidium amansii to zero at about 80% dehydration; thus, air exposure could also restrict the vertical extent of this species during summer. However, perhaps also other factors along with, or interacting with desiccation could regulate the vertical distribution of some species. Since C. pulchellum on the southwest coast of France is upper littoral in shaded places, eulittoral in exposed places, and sublittoral in sheltered places, perhaps interactions between light intensity, temperatures, water movement and nutrients could explain that particular pattern of distribution. Interestingly enough, as will be discussed later, this multiple interaction may explain the horizontal distribution of species of Gelidium and Pterocladia in Hawaii (Santelices, 1977) and summer bleaching of intertidal and subtidal populations of several species of Gelidium at different latitudes (Seoane-Camba, 1965; Yamada and Iwahashi, 1964; Yamada, 1972).

No quantitative study seems to have been performed to explore the causes of lower vertical distributional limits of species of Gelidium and Pterocladia, although biotic interactions could account for them. Grazing could explain the sharp lower limit (followed by bare rock) of some species such as Gelidium sp. from Hawaii (Doty, 1967) or Gelidium cartilagineum from Teneriffe (Lawson and Norton, 1971). Interspecific interference could explain the lower limits of species abruptly contacting other algal species. In one of these situations, Kastendiek (1982) showed that competitive interference by Halidrys dioica could limit the occurrence and distribution of Pterocladia capillacea at around 2.3 m depth in Santa Carolina Island, California. Perhaps different tolerance limits to abiotic extremes affecting competitive abilities could explain the occurrence of successive belts of Gelidium and/or Pterocladia so commonly found in intertidal shallow subtidal habitats. At least, this seems to be the case in the zonation pattern of four belt-forming species of Gelidium that are common in intertidal and shallow subtidal habitats of central Chile. The uppermost belt is formed by G. pusillum which, under experimental conditions, had a higher temperature optimum for growth than any of the other species of Gelidium (Oliger and Santelices, 1981). The lowest belt is formed by G. rex, the species with lowest temperature and light tolerance, while G. lingulatum and G. chilense co-occur at the middle intertidal belt. Interspecific interference between these last two species modifies their respective vegetative and reproductive stocks and their patterns of morphological variation (Montalva and Santelices, 1981). G. lingulatum is most abundant in summer due to its higher growth rates under high light intensities.

Table 1

Common species of Gelidium and Pterocladia forming intertidal and subtidal belts

Species	Place	Fishing area number	Local distribution	References
G. amansii	Japan	61	Common from zero to -60 cm below	Matsuura, 1958
	Japan	61	Lower littoral or sublittoral from -30 to -200 cm below zero level	Saito and Atobe, 1970
	Japan	61	Down to 20 m deep	Okasaki, 1971
	China	61	Intertidal and subtidal	Tseng, Zhou and Pan, 1981
G. attenuatum	Spanish west Africa	34	Intertidal	Primo, 1953
	South West of France	37	From zero level to -5 m	Van den Hoeck and Donze, 1966
G. arbuscula	Canary Island	34	Forming a fringe some 45 cm wide, 20 to 40 cm below half tide level	Rodríguez, 1953; Prud'homme van Reine, Weisscher and Duineveld, 1981
	Teneriffe	34	Forming a girdle of about 0.3 m of vertical height in the intertidal region	Lawson and Norton, 1971
G. cartilagineum	Teneriffe	34	Forming a thick belt down to low water and below. It can extend to -2 m and decreases with depth with clear cut upper and lower limits	Lawson and Norton, 1971
	Canary Island	34	From about 65 cm below half tide level, extending down further than the eye can reach	Rodríguez, 1953
	South Africa	47	Important member of the intertidal zone along the coast of False Bay	Ohno, 1977
G. caulacantheum	New Zealand	81	Occupies a belt in shady places on rocks at mean high water of neap-tides	Chapman, 1966
G. chilense	Chile	87	Lower part of intertidal zone (as G. filicinum)	Guiler, 1959

Table 1 (cont'd)

Species	Place	Fishing area number	Local distribution	References
G. chilense (cont'd)	Chile	87	Extends in the intertidal between 1 and 2 m above zero level	Santelices and Montalva, 1983
G. coulteri	Washington to Baja California, USA	67, 77	Abundant intertidally on rocks or in tufts on mussel shells	Stewart, 1976
G. crinale	South East coast of Curaçao	31	Lowest littoral zone	Van den Hoeck and Donze, 1966
	Spanish west Africa	34	In pools at low tide level	Primo, 1953
G. divaricatum	Japan	61	From 20 to 60 cm above zero level	Matsuura, 1958
	China	61	It grows on rocks in the upper littoral zone	Tseng, Zhou and Pan, 1981
G. glandulaefolium	South Australia	57	1 to 3 m below water	Shepherd and Womersley, 1970
	West Island, South Australia	57	Abundant between 0 and 3 to 5 m deep	Womersley, 1972
G. japonicum	Japan	61	From zero to -60 cm	Matsuura, 1958
G. latifolium	South of France	37	Upper sublittoral	Van den Hoeck and Donze, 1966
	Spain, Asturias	27	Co-dominant intertidal species between 0 and 0.8 above zero level	Anadon, 1983
			In exposed habitats between 0 and + 1.5 m	Fernández and Niell, 1981, 1982
	Malta	37	Abundant between 0 and 5 m deep	Giacone et al., 1972
	Norway	27	At depths of about 0.5 to 1.0 m in shallow, well protected bays	Jorde, 1966
G. lingulatum	Chile	87	Common intertidal species extending between 1 to 2 m, in exposed habitats	Oliger and Santelices, 1981; Montalva and Santelices, 1981
G. pacificum	Japan	61	From zero to -60 cm below	Matsuura, 1958
G. pectinatum	Italy, Sicily Channel	37	Abundant between 0 and 20 m	Giacone et al., 1972

Table 1 (cont'd)

Species	Place	Fishing area number	Local distribution	References
G. pluma	Hawaii	77	From zero tide level to 1.5 m below	Santelices, 1977
G. pristoides	South Africa	47	Middle and lower intertidal levels	Isaac and Molteno, 1953
G. pulchellum	South West coast of France	37	Eulittoral, from zero to 1 m above in exposed places and sublittoral in sheltered places	Van den Hoeck and Donze, 1966
G. pusillum	Japan	61	From 20 to 60 cm above zero level	Matsuura, 1958
	Sierra Leone	34	In lower part of the mid littoral zone	Lawson, 1957
	Trinidad	31	10-20 cm above zero level, forming mixed turf with other algae	Richardson, 1969
	Palao	77	In the lower littoral region, in somewhat sheltered localities, on a narrow reef flat	Kanda, 1944
	Spain	27	Middle and lower littoral (0 to + 1.5 m)	Seoane-Camba, 1965; Fernández and Niell, 1981, 1982
	New Zealand, Auckland	81	Often confined on open mid-littoral to moist and shady cliffs	Dellow and Cassie, 1956
	Australia, Victoria	81	Upper and half mid littoral	Bennett and Pope, 1953
	Chile	87	Upper intertidal species extending up to 3.0 m above zero in exposed areas	Oliger and Santelices, 1981
	Hawaii	77	10-40 cm above mean low tide level	Santelices, 1977
	New Zealand	81	Abundant inter-tidal species	Miller and Furneaux, 1982
G. pusillum	British Columbia to Ecuador	67, 77	Throughout inter-tidal and also subtidal	Stewart, 1976

Table 1 (cont'd)

Species	Place	Fishing area number	Local distribution	References
G. rex	Chile	87	Intertidal-subtidal fringe, from -1.0 to + 0.5 m. Often in very exposed rocky surfaces under the shade of Lessonia nigrescens	Santelices and Abbott, 1985
G. robustum	Baja California, Mexico	77	Rocky shores exposed to strong waves from medium level of intertidal zone to a depth of 15-17 m confined primarily to areas where cold upwelling waters occur	Dawson, Neushul and Wildman, 1960; Guzmán del Proó, 1969; Barilotti and Silverthorne, 1972; Guzmán del Proó and de la Campa de Guzmán, 1979
G. serrulatum	Venezuela	31	On intertidal rocks in strong surf, about 2 km east of Boca del Rio, Capúrano, Estado de Sucre	Ganesan, 1971
G. sesquipedale	Spanish west Africa	34	Intertidal	Primo, 1953
	Spain	27	Lower littoral (0 - 0.5 m) of Asturias, codominant with Saccorhiza, Cystoseira and G. latifolium	Anadon, 1983
			Also in exposed sublittoral areas	Fernández and Niell, 1981, 1982
			Sublittoral	Seoane-Camba, 1965
			Abundant at 8 m off La Coruña	Alvarez et al., 1978
	Portugal	27	Frequent and abundant at the Arrabida coast	Melo and Santos, 1979
	South west of France	37	From zero level to -15 m	Van den Hoeck and Donze, 1966
G. sesquipedale	Morocco	34	Reen places Cystoseira and G. arbuscula at the level just above low water mark	Prud'homme van Reine, Weisscher and Duineweld, 1981
G. spathulatum	Spain	27	Lower littoral	Seoane-Camba, 1965
	Morocco	34	On rocks, covered during low tides	Dangeard, 1960
	Spanish west Africa	34	Low intertidal	Primo, 1953
G. vagum	Japan	61	In the upper sublittoral belt	Tokida, 1954

Table 1 (cont'd)

Species	Place	Fishing area number	Local distribution	References
P. bartlettii	Teneriffe	34	From zero level to 10 cm above	Lawson and Norton, 1971
P. caerulescens	Hawaii	77	Intertidal and subtidal	Santelices, 1977
P. capillacea	South west coast of France	37	Upper sublittoral	Van den Hoeck and Donze, 1966
	Mediterranean coast of Israel	37	One of the dominant or subdominant species in vertical walls between 0-2 m deep	Lundberg, 1981
	Italy	37	Common intertidal member along the Sicily coast (as P. pinnata)	Amico et al., 1979
	Azores	27	Grows in abundance at depths of -1 to -5 m (as P. pinnata)	Fralick and Andrade, 1981
	Malta	37	Almost pure stands between 2 and 5 m deep in calm areas and high nitrogen content	Giacone et al., 1972
	Brazil, Ubatuba	41	Common shallow subtidal	Oliveira and Sazima, 1973
	California to Baja California, USA	77	Intertidal and subtidal to 20 m deep	Stewart, 1976
	Cameroon, Ghana and Senegal	34	Lower eulittoral	Lawson, 1966
	Egypt	37	Grows profesely along the sublittoral belt of the rocky coast of Egypt	Rao, Thomas and Subbaramaiah, 1976
	Japan	61	From zero to -60 cm below	Matsuura, 1958
	Victoria, Australia	81	Infralittoral fringe	Bennett and Pope, 1953
	South Australia	81	Upper sublittoral extending to -4 m	Shepherd and Womersley, 1970
	West Island, South Australia	81	Low tide down to -3 m	Womersley, 1972
	New Zealand	81	Abundant intertidal and subtidal species	Miller and Furneaux, 1982
P. lucida	Wellington, New Zealand	81	Common in deep water (5-8 m)	Hicks, 1977

Several morphological differences have been reported to be connected with vertical distribution. One of the first of these reports was the one by Dixon (1958), indicating that the thalli of Gelidium latifolium exposed during low waters of spring tides were shorter in height and annual, while those never exposed were longer and could persist for more than one year. Similar reports have been reported thereafter for several other species of Gelidium from Europe (Dixon, 1963a), Pterocladia capillacea from San Diego (Stewart, 1968), G. sesquipedale from Spain (Seoane-Camba, 1965), G. rigidum from Fiji (Chapman, 1977), P. caerulescens from Hawaii (Santelices, 1978), G. filicinum and G. lingulatum from central Chile (Montalva and Santelices, 1981) and G. spathulatum from Spain (Gómez-Garreta, Ribera Siguan and Seoane-Camba, 1982). Desiccation and decreased photosynthesis, coupled with decreased diffusion and restricted fertilizer absorption during low tides, could explain the size reduction of these populations.

2.3 Effect of Ecological Determinants

Tolerance limits of different species of Gelidium and Pterocladia to ecological factors have been determined from field measurements of abiotic factors correlated with local patterns of ecological distribution. In some cases, laboratory experiments have tested the biological effects of these field correlations and defined physiological optima for growth.

2.3.1 Light intensity

Light intensity has often been mentioned as determining distribution and growth of these species. Numerous authors have indicated that Pterocladia capillacea, P. caerulescens and several species of Gelidium became conspicuously larger or dominant in shaded habitats of the littoral zone of Auckland (Dellow and Cassie, 1956), California (Stewart, 1968), France (Van den Hoeck and Donze, 1966; Dangeard, 1960), Palao (Kanda, 1944), South Australia (Womersley and Edmonds, 1958; Shepherd and Womersley, 1970), Spain (Seoane-Camba, 1964, 1965; Donze, 1968) and Hawaii (Santelices, 1978). Larger and darker thalli under shaded conditions have been reported for Gelidium populations in Samoa (Doty and Morrison, 1954) and for populations of Pterocladia capillacea from San Diego (Stewart, 1968) and Hawaii (Santelices, 1978). Bleaching of thalli has been reported (Seoane-Camba, 1965; Shepherd and Womersley, 1970) in summer populations of Gelidium and Pterocladia from Japan, Spain, Hawaii and Chile (Seoane-Camba, 1965; Yamada, 1972; Santelices, 1978, Montalva and Santelices, 1981) and in the upper intertidal populations of Pterocladia capillacea from Australia. Light measurements in the field have reported that these species occur under intensities as low as 500 meter candles (G. pusillum, in New Zealand, Dellow and Cassie, 1956) or under 20-25% of incident light (P. capillacea in Hawaii, Santelices, 1978). Laboratory experiments have also shown the species of Gelidium to be more efficient under low light intensities. Thus, Gelidium caulacantheum had a greater photosynthesis rate at 800 ft-candles than at 2 000 ft-candles (Chapman, 1966), while the saturation light intensity for G. amansii was below 5 klux (Ogata and Matsui, 1965). Compared to the saturation values of 21 klux for upper intertidal algae such as Ulva or Porphyra, the saturation intensity for G. amansii is rather low. In Pterocladia capillacea, the growth rates found under overcast skies, with an irradiance of 50-70%, were greater (Strömgren, 1984) than during 100% sunshine. The only different result is the one reported by Tseng, Zhou and Pan (1981), indicating saturation levels as high as 40 klux for G. amansii. Tseng, Zhou and Pan (1981), however recognized that, after having been laboratory-cultured for 15 days, G. amansii had its light saturation value decreased to about 18 klux, which shows that the photosynthetic saturation in this species was well adapted to decreases in light intensity.

Growth limitation due to low light intensity has been experimentally tested at least twice and the results further illustrate the low light tolerance of these species. Spores of G. amansii incubated under dark conditions by Ohno and Arasaki (1969) could be maintained alive for up to 3 weeks, regardless of the temperatures used (in the range of 5 to 20oC). Likewise, field experiments performed in 1974 at 10 m depth at Point Lomas and Palos Verdes, southern California indicated (Barilotti, 1980) no significant differences in growth rates between thalli grown over black plastic and those grown over mirrors. Furthermore, laboratory experiments tend to indicate that some of these species can adapt to different light intensities by modifying their growth patterns (Felicini, 1970). Under low light intensities, (750-1 000 lux), Pteroclaida capillacea formed creeping filaments, while under higher light intensities there was increased formation of erect fronds.

Damaging effects due to high light intensity have been more frequently reported for these species. Perhaps the commonest field observation is bleaching of the thallus followed by necrosis under high light intensities in summer, or in high intertidal populations (Yamada, 1961, 1964, 1967; Seoane-Camba, 1965; Shepherd and Womersley, 1970). More recently, however, laboratory and field experiments have indicated that the bleaching effects generally attributed to high intensities actually result from a complex interaction between light intensity, temperature, nutrients and water movement (Santelices, 1978). The growth rates and bleaching of Pterocladia capillacea and P. caerulescens from Hawaii were directly affected by light intensity and water movement. These two main factors not only acted alone but interacted with each other. When one of the two factors was

below its threshold, it did not allow the other factor to express its effects on the growth rate of the species. In these experiments, nutrient enrichment effectively compensated for water movement, as both species attained maximum growth at comparatively low water movement intensities when grown in fertilizer-enriched media. Enhancement of diffusion resulting from higher water movement or greater enrichment allowed the two species to use higher levels of light and temperature more efficiently as shown by faster growth and, at least in the laboratory, counteracted the bleaching effects of high light intensity (Santelices, 1978).

The effects of light on pigment concentration have been studied (Seoane-Camba, 1964, 1965) in three species of Gelidium from Spain. The chlorophyll-a content of G. pusillum, G. spinulosum and G. sesquipedale was correlated with the cloudiness and light intensities occurring at different times of the year. Seoane-Camba looked for correlations between light intensities occurring several days before the collection of algae and the chlorophyll-a content at the time of collection. He found that during the summer, when the air temperature was between 22 and 27°C, the chlorophyll-a content correlates well with light conditions occurring ten days previously. During winter, when the air temperature oscillated between 13 and 19°C, the correlation was best with light intensities occurring 25 days previously. Finally, during fall and spring, when the air temperature was about 20 to 22°C, the correlation was closer with the light values of 20 days previously. He concluded that adaptation of the thalli to external energy conditions is higher in summer than in winter, probably depending on temperature changes; therefore, he added, the adaptation mechanisms should be related to physiological changes which he did not identify.

Light quality effects on Gelidiaceae are described in a report by Katada (1949) indicating that the growth of sporelings of Gelidium amansii was better under blue light than under white light. No measurements of the total energy per unit surface were reported in this work. Effects of light on reproduction will be discussed in Section 3.2.

2.3.2 Temperature

Some experimental studies have intended to relate differences in temperature tolerance and optima for the species of Gelidium and Pterocladia with vertical distribution. In one such study Schölm (1966) found that the shallow subtidal thalli of Pterocladia capillacea (as P. pyramidale) from 3 m depth could resist for 30 minutes exposures up to 38°C whereas the deeper subtidal thalli of Gelidium cartilagineum and G. nudifrons inhabiting 13-14 m depth could resist only temperatures below 30-32°C. More recently, Oliger and Santelices (1981) found that the upper intertidal G. pusillum had higher temperature optima for growth (20°C) than the shallow subtidal G. rex (15°C). Studies of temperature effects on the species of Gelidium and Pterocladia have more often related this factor to their temporal distribution.

Species presence, growth of individual thalli, population growth, sexual reproduction, tetraspore formation, shedding and germination, and agar deposition are all aspects of the biology of these algae in which a seasonal cycle has been found in most places of the world. A few laboratory studies have provided experimental evidence indicating that temperature is important. However, most studies lead to the conclusion that temperature is often correlated with, but not necessarily involved as, the controlling factor. What follows is a summarized review of the pertinent evidence. Temperature control of reproduction is discussed under section 3.2.

Seasonal occurrence of Gelidium has been reported in two temperate localities. Gelidium crinale was present (Conover, 1958) at Great Pond, Massachusetts, only from May to October, reaching its maximum standing crop from June to September. The effects of low water temperature and the subsequent ice formation were thought to be responsible for the near extinction of the species during the winter months. Similarly, at Chesapeake Bay, the same species was present (Zaneveld and Barnes, 1965) only during the summer months. The appearance of this species in March and its subsequent increase in frequency was related to the increase of surface water temperature. In fact, apart from March, the species was found only during the three warmest months of the year (23 to 25°C), which suggests that temperature is a regulating factor.

Seasonal phenomena in the growth of the Gelidiales have been reported from both qualitative and quantitative studies. In England, the individuals of Pterocladia capillacea undergo (Dixon, 1963, 1963a) a growth cycle each year. The axes, initially cylindrical in outline, are formed in spring. Their growth in length soon stops, but the growth in breadth continues so that the axes of the mature thalli are broad and flat. The erect frond persists for a number of years and each spring growth recommences. The early elongation of the thallus leaves a mark which can be later recognized and which has been used (Seoane-Camba, 1969) for population studies of growth and longevity. A similar seasonal cycle has been reported for Gelidium corneum in the Texas lagoons (Conover, 1964), for G. sesquipedale in Spain (Seoane-Camba, 1969) and for P. capillacea in (Dixon, 1970) New Zealand. Changes in growth rate through the year have been noted in other species, although the form of the thallus apparently does not change with the season. Thus, the growth rate of the sublittoral G. robustum (as G. cartilagineum) from Baja California was (Guzmán del Proó and de la

Campa de Guzmán, 1969; Barilotti and Silverthorne, 1972) higher in September. Similarly, in the province of Sagami, Japan, the population growth, estimated from the appearance, vigor and decay of individuals of seven species of Gelidiaceae, was found (Matsuura, 1958) to start increasing in March and to reach its maximum in May or June. The cover values obtained from populations of G. amansii from Japan started increasing (Saito and Atobe, 1970) during or after winter and reached their maxima before summer. Finally, it should be mentioned that so far, as found in the literature, the only cases in which seasonal pattern of growth is absent have been observed in the populations of P. capillacea from San Diego, California (Stewart, 1968) and in two species of Gelidium from central Chile (Montalva and Santelices, 1981).

The hypothesis that seasonal growth of the Gelidiales could be temperature-related has arisen mostly from field temperature values correlated with algal growth. Thus, on the reefs of the province of Sagami, Matsuura (1958) found that the increase in growth rate of seven species of Gelidiaceae was coincident with a rise of temperature from 13 to 20°C. The species disappeared, however, at temperatures above 25°C. Similarly, at Usujiri, Japan, Gelidium amansii reached (Saito and Atobe, 1970) its maximum frequency and cover at 15°C (September), although the maximum temperature was close to 20°C during August. Finally, the seasonal increase in growth of G. robustum from Baja California was also correlated (Barilotti and Silverthorne, 1972) with an increase in sea water temperature.

It is difficult, mainly due to the absence of data, to evaluate the importance of light or other factors in all these reports as alternative explanations of seasonality. Incident radiation was measured by Conover (1964) and transparency by Matsuura (1958). Although these last authors recognized temperature as the most probable seasonal factor, Matsuura remarked on the need of further, more direct, experimental evidence.

Laboratory studies testing the effects of temperature on photosynthesis of species of Gelidium in general, indicate that they have a broad tolerance range. In Gelidium amansii, photosynthesis steadily increases up to 30°C (Yokohama, 1972), although there seem to be no significant differences in the photosynthetic rates shown by this species between 15° and 30°C. Photosynthesis falls abruptly above 35°C. A wide temperature range was shown also by G. coulterii with optimum temperatures between 20 and 35°C. The upper limit to photosynthesis in this species occurred between 33 and 42°C, whereas a fairly low rate was recorded at 3°C.

Experimental studies on temperature effects on growth have however shown a much more reduced range. Pterocladia capillacea and P. caerulescens from Hawaii could grow between 20 and 30°C (Santelices, 1978a) while four temperate species of Gelidium could grow between 10 and 20°C (Oliger and Santelices, 1981).

2.3.3 Water movement

The relation between local distribution of species of Gelidium and Pterocladia and water movement is probably one of the most frequently described ecological relationship of the group. From some taxonomic reports and in many ecological works, the species of these genera have been found in "exposed situations" at different levels of the shore. However, in southern Australia, Gelidium pusillum was found (Womersley and Edmonds, 1958) living on muddy substrata in places with slight water movement, and G. latifolium occurs in Norway (Jorde, 1966) in a shallow, well protected bay. In most places, in both temperate (Tseng, 1947; Primo, 1953; Ercegovic, 1957; van den Hoeck and Donze, 1966; Donze, 1968; Shepherd and Womersley, 1970) and tropical latitutes (Hodgkins and Michel, 1961; van den Hoeck, 1969; Umameheswara-rao, 1969; Lawson and Norton, 1971), the species of Gelidium and Pterocladia are associated with high levels of water movement (see also Table 1). Some authors have attempted to further qualify the term "exposure" as low, moderate or very high, and the Gelidiaceae have been generally ranked in moderate to high water-movement habitats, "highly exposed" being a frequently described situation. They do not seem to be very successful under extremely high levels of water movement, exemplified by a Gelidiaceous association (Pterocladia capillacea in south Australia), which was observed (Shepherd and Womersley, 1970) to be displaced by coralline algae under conditions of extreme surge.

Quantitative, integrated measurements of water movement applicable to benthic situations are (Doty, 1971) relatively recent, and often impossible to apply in wave-beaten habitats. Consequently, almost no quantitative data are available for these species. The only available information found is the increase in standing stock of Pteroclaida capillacea in some Hawaiian reefs, which correlates positively with increments in water movement measured as dissolution rates of calcium sulfate blocks, and experimental data obtained with this species and P. caerulescens simulating different water movement intensities by using especially adapted rotary shakers (Santelices, 1978a). Growth rates in both species increased with increasing levels of water movement up to an optimum water movement value.

The anatomical adaptations of these species to intense water movement seemingly involve internal and external morphology. Already in 1936, Feldmann and Hamel interpreted the presence of internal hyphae as a special adaptation to withstand water movement. More recently, Anderson and Charters (1982) studied the significance of the branching pattern in relation to water motion in G. nudifrons. They noticed that this species has a thallus composed of rodlike branches which are closely spaced, but sufficiently open so that water flows freely through them. The plant strongly suppresses turbulence in the flow entering its thallus and at the same time generates micro-turbulences of its own at velocities above critical values, varying from 6 to 12 cm/s^{-1}, depending on the diameter and spatial density of the branches, due to the formation of systematic vorticity and the wakes of individuals branches. This transition in the flow induced by the branches is suggested by Anderson and Charters (1982) to be a phenomenon of considerable adaptative significance, because the turbulence generated by the plant itself or by neighbouring plants may be the only turbulence in the water motion past the plant that is of the right scale to enhance nutrient uptakes and affect the exchange of gases and solutes.

2.3.4 Salinity

Field measurements of salinity tolerance seem to indicate that some species of Gelidiaceae can withstand dilutions more easily than increases in salt concentration. For example, Gelidium pusillum from Sierra Leone occurred in places with an average salinity (Lawson, 1957) of 26.3°/oo in surface waters and of about 31.46°/oo at 3 m depth. Similarly, Gelidium corneum from the Texas lagoons, was found (Conover, 1964) in waters of salinities as low as 13°/oo. In Hauula, on the northern shore of the island of Oahu, Hawaiian Archipelago, Pterocladia caerulescens occurs on the nearshore edge of reefs where salinity decreases down to 20°/oo at low tides during the months of less water movement, probably due to freshwater influx from streams near the edge of the reef (Santelices, 1978a). By contrast, only G. corneum and G. crinale have been reported from places with salinities higher than normal sea water. Both species were found (Conover, 1964), in the Texas lagoons, reaching a maximum salinity of 37°/oo.

Experimental studies have shown that the range of salinity tolerance of various species of Gelidium and Pterocladia normally exceeds the salinity variation found in the field and that the tolerance limits can be modified by temperature. Thus, four species of Gelidium common in intertidal and shallow subtidal habitats in central Chile can grow at salinities between 25 and 45°/oo (Oliger and Santelices, 1981). Pterocladia caerulescens from Hawaii could tolerate salinities from 20 to 60°/oo but the optimum values for growth changed as a function of temperature. They were 30°/oo at 20°C and 24°C, 35°/oo under 28°C, and 40°/oo under 32°C. In P. capillacea from Hawaii, both the tolerance limits and the optimum growth value were affected by temperature. This species could grow from 10°/oo to 50°/oo salinity at 20°C and up to 80°/oo salinity at 28°C and 32°C (Santelices, 1978a). In the case of sporelings of Gelidium amansii, growth decreased above and below normal sea water concentrations, decreasing more at 25°C than at 10°C (Ohno, 1969). Additional experimental studies on Gelidium amansii from Japan have shown that salinity effects depend also upon duration of exposure and temperature. Exposures for 24 hours to hypotonic solutions from 0 to 25% sea water produced (Ogata and Takada, 1968) irreversible changes in respiration, while similar treatment in hypotonic solutions above 25% normal sea water produced reversible results. The respiration rates of the treated thalli were not significantly different, upon recovery, from the controls in normal sea water. Hypertonic solutions of 1.5 and 2 times the sea water concentration, on the other hand, produced irreversible rises in the respiratory rate of G. amansii.

2.3.5 Substratum

Rocky surfaces, sometimes precipitous and with steep slopes, have been described (Kanda, 1944; Primo, 1953; Womersley and Edmonds, 1958; Taniguti, 1962; Richardson, 1969; van den Hoeck, 1969; Shepherd and Womersley, 1970) as the most frequent attachment substrata for various species of Gelidium. Exceptions to this general trend are G. pusillum, occurring (Womersley and Edmonds, 1958) on muddy substrate in South Australia and G. crinale in (Seoane-Camba, 1965) sandy places on the coast of Cadiz.

Possible morphological effects of substratum have been reported (Dixon, 1958a) for Gelidium latifolium in England. When this species occurs on reefs or large rocks, the erect fronds arise at intervals from well-developed creeping axes, whereas the specimens attached to small stones embedded in stretches of sandy mud between the reefs are tufted, with minute creeping axes.

Species of Gelidium and Pterocladia seemingly have preference for some types of substratum. A surprisingly high number of reports (see Table 2) have species of these genera occurring in close proximity to crustose coralline algae. This apparently general characteristic has not been investigated by any author and consequently the nature of the association is unknown. However, two different working hypotheses could be advanced at this time in order to explain the crustose coralline-Gelidium/Pterocladia relationships. The first idea arises from the studies (Dixon, 1958a)

Table 2

Species of Gelidium and Pterocladia associated with coralline algae

Species	Place	Fishing area number	Obervation	References
G. amansii	Japan	61	In order to expand the growing areas, stones should be placed on sandy bottoms, in and around the growing area. Soon after calcareous algae such as Lithothamnion appear on the stones and spores of Gelidium grow on them	Suto, 1974
G. attenuatum	South west coast of France	37	Firmly attached to Mesophyllum lichenoides	Van den Hoeck and Donze, 1966
G. glandulaefolium	South Australia	57	On slight to moderate surge. When surge is more severe, the association is displaced by coralline algae	Shepherd and Womersley, 1970
G. pulchellum	South west coast of France	37	On rocks predominantly covered by Lithothamnion and Dermatolithon often growing attached to encrusting algae	Van den Hoeck and Donze, 1966
G. pusillum	Sierra Leone	34	The Lithothamnia zone consists of rather patchy pink encrusting coralines interfaced and superimposed by a number of very small algae which often form a turf and among which is this species	Lawson, 1966
Gelidium sp.	Hawaii	77	The zone just below zero level is underlain by smooth crustose coralline algae and often covered by Gelidium	Doty, 1967
	West coast of India	51, 57	There is a Gelidium-Polysiphonia belt which marks the last portion of the midlittoral. The gravelly though calcareous strate shows comparatively a better development of the belt	Misra, 1960

Table 2 (cont'd)

Species	Place	Fishing area number	Observation	References
P. bartlettii	Trinidad	31	With crustose lithothamnia and small accounts of Enteromorpha sp.	Richardson, 1969
P. capillacea	West Australia	81	Together with encrusting lithothamnia and other algae	Womersley and Edmonds, 1958
	California, USA	77	Abundant together with Corallina officinalis var chilensis between + 0.15 and - 0.15 m	Littler and Murray, 1975

of tow species of Gelidium and one species of Pterocladia from England. The creeping axes in several instances were found to survive the summer sunlight in the crevices of the rock, below a cover of crustose coralline algae. Regeneration and growth of erect fronds from creeping axes are common in these algae. Under unfavourable environments, vegetative propagation is a frequent method of colonization and dispersal. Intense light is also known to damage some species. Therefore a crustose algal cover, acting as a light screen, could allow the survival of creeping axes which would later regenerate and produce erect fronds.

An alternative explanation arises from the observations by Shepherd and Womersley (1970) that the Pterocladia capillacea association occurring in south Australia under moderate surge can be displaced by coralline algae when the surge is more severe. This observation leads to the possibility that crustose coralline algae and Gelidiaceae have similar or closely related optima for some ecological factors such as water movement; therefore, both groups would tend to occur in the same habitat, perhaps competing for substrate and light. More severe conditions, such as extreme surge in this case, either directly limit one of the competitors, or favour success of the other competitor, resulting in one of the groups being displaced at a given site.

2.3.6 Epiphytism and parasitism

Epiphytes and presumptive parasites can occur on several members of Gelidiaceae. Epiphytes have been observed (Seoane-Camba, 1965, 1982; Cendrero and Ramos, 1967; Barilotti and Silverthorne, 1972) especially on the larger subtidal thalli of Gelidium, supposedly reducing the amount of available light and decreasing the agar yield of the population.

Parasites have also been reported on these species. Three genera and about seven species of red algae have been found (Fan and Papenfuss, 1959) as specific parasites of various members of the Gelidiaceae. Species of Gelidium, Pterocladia, Suhria and Beckerella are among the hosts, and all parasites so far reported belong to two families of the order Cryptonemiales. The nature of the association, supposed to be parasitic, has not been tested so far.

2.3.7 Grazing

Direct evidence indicating that fishes consume Gelidiaceae was found by Dawson, Aleem and Halstead, (1955), studying the marine algae from Palmyra Atolls. Four species, namely Gelidium pusillum, G. crinale, Pterocladia sp. and Gelidiella stichidiospora were found in the alimentary tracts of reef fishes. The latter two species were estimated to be among the most abundant food items of Acanthurus triostegus and A. aliala, respectively. In Spain, similar studies reported (Seoane-Camba, 1965) rhizoidal portions of G. spinolosum and G. pusillum in the stomach and intestine of four herbivorous fishes, and in the Virgin Islands, Randall (1967) and Earle (1972) indicated that G. corneum and several other unidentified species of Gelidium were eaten by, and frequently present in the intestines of several species of fish.

A few reports tend to indicate that some species of Gelidium and Pterocladia stand low in preference among the food items of invertebrate grazers. For example, the abalone Haliotis cracherodii loses weight when experimentally fed with these algae (Leighton and Boolotian, 1963). The food preference shown by the abalone toward Gelidium purpurascens and Pterocladia capillacea, as

compared to other species of benthic algae, was extremely low and therefore the loss of weight by the abalone was interpreted as due to lack of feeding. Likewise, Gelidium cartilagineum seems to be a less preferred item in the littoral and sublittoral region of Teneriffe. The rocky intertidal surface of this place is relatively barren of algae supposedly due to the grazing activity of the sea urchins, Arbacia lixula and Paracentrotus lividus (Lawson and Norton, 1971). At this same place, however, G. cartilagineum was very abundant and one of the dominant belt-forming species. This could perhaps be interpreted as an indication that grazing pressure is low on G. cartilagineum.

In spite of the above reports, the low preference value for species of Gelidium and Pterocladia does not seem to be a general rule among invertebrates. In New Zealand, gut analyses of the abalone Haliotis australis showed (Poore, 1972) that about 20% of the food content was Pterocladia lucida which, compared with other algal species, was surpassed in preference only by Hymenocladia lanceolata which constitutes almost 38% of the total amount of food of this abalone. Likewise, gut content analysis of Aplysia punctata from the intertidal levels of the Ria de Vigo, Spain, revealed G. pulchellum to be among the most frequent food items out of 44 algal species found (Niell, 1977). In Japan, G. amansii and G. divaricatum were the only two species among 14 Rhodophyta to stimulate exploratory and feeding behaviour in young individuals of the abalone Haliotis discus (Harada and Kawasaki, 1982), while Jernakoff (1983) described Gelidium pusillum on the rocky intertidal shores of southeastern Australia as occurring in small clumps, which probably reflected escapement from grazing at the spore level. In this respect it is interesting to note that Fenical (1975) found no significant formation of halogenated metabolites in the species of Gelidium that he investigated, a finding confirmed by Anderson and Velimirov (1982) with Gelidium sp. from South Africa.

2.3.8 Competition

Early observations and experiments on possibly competitive effects of species of Gelidium and Pterocladia were performed by Seoane-Camba (1966) and Cendrero and Ramos (1967). However, no clear conclusion was reached. More recently, two studies have shown interspecific interference to be an important factor determining the occurrence and abundance of these species. In exposed localities of central Chile, G. lingulatum and G. chilense overlap in vertical and temporal distribution. The stocks of these two species have little seasonal variations. The stock variations of each species rather indicate a significant negative correlation with the stock variations of the other species. In both species there is a continuous presence of tetrasporangial thalli throughout the year, and a direct correlation between total standing stock and tetrasporangial standing stock exists. Therefore, the negative correlation between both species also affects the amounts of tetrasporangial thalli produced and their reproductive potentials (Montalva and Santelices, 1981).

More recently, Kastendiek (1982) found the occurrence of Pterocladia capillacea in shallow subtidal habitats of Santa Catalina Island, California, to be dependent on interspecific competition. In this place, P. capillacea occurs in a narrow band of substratum from 0.3 to 2.3 m below mean lowest low water (MLLW), together with Eisenia arborea and Halidry dioica. E. arborea forms a canopy and excludes H. dioica from areas beneath it. P. capillacea occurs in the space beneath the E. arborea canopy. Upon canopy removal, H. dioica grows adventitiously, excludes P. capillacea and preempts all space on the substratum. However, P. capillacea is not physiologically restricted to being an understory organism. When the canopy is experimentally removed and H. dioica is prevented from entering the area, P. capillacea fluorishes. P. capillacea persists in this community because of its ability to utilize the refuge from its superior competitor, H. dioica, afforded by the canopy of E. arborea. Kastendiek (1982) has recognized this as an example of competitor-mediated coexistence.

2.4 Nutrition and Growth

2.4.1 and 2.4.2 Assimilation and respiration

Physiological processes in species of Gelidium and Pterocladia have been comparatively less studied. Photosynthetic rates in these species are affected by light intensity, temperature, nitrogen status of the tissues, emersion to air and thallus crowding. Respiration rates are affected by thallus crowding and salinity (Ogata and Takada, 1968).

Studies showing the effects of light intensity (Ogata and Matsui, 1965; Chapman, 1966; Hansen, 1980) and temperature (Yokohama, 1972; Hansen, 1980) on photosynthetic rates of species of Gelidium have been already referred to in the previous sections. Emersion to air should be added as a third important factor. Thus, the net photosynthesis of G. coulteri from California was 4-5 times greater when the thallus was submerged rather than emergent (Hansen, 1983). This depressed net photosynthesis of G. coulteri in air was thought to be related to higher levels of oxygen and lower levels of bicarbonate in air as compared to sea water. Nitrogen status of the tissues is also important, as plants taking in nitrogen at luxury levels showed (Macler, 1986) C14 fixation rates several folds higher than those seen in plants starved for nitrogen. Finally, experimental studies

with Gelidium pusillum indicated that clumped forms of this species produced (and respired) at only half the rate of separate individuals (Littler and Arnold, 1980). This phenomenon was attributed to competition for CO_2 and to mutual self-shading by overlapping thalli, even when surrounded by relatively large volumes of seawater.

As in many other species of macroalgae, photosynthetic rates undergo temporal and spatial variation in the species of Gelidium and Pterocladia. For example, at Santa Catalina Island, California, Pterocladia capillacea shows highest productivity during winter with a clear reduction in spring and summer. In the case of G. pusillum from the same place, the highest productivity occurred in summer (Littler, Murray and Arnold, 1979). This study also showed that in these species, maximum productivity and maximum standing stock do not always occur at the same season. This was the case of G. pusillum, a species which, in this locality, showed reduced stocks during summer.

2.4.3 Nutrition

Indirect evidence suggesting high nitrogen and phosphorus tolerance in several species of Gelidium and Pterocladia has arisen from pollution studies. At different latitudes where N and P levels had increased due to domestic pollution, various authors found that these species have survived the fertilizer changes and, in some areas, even increased their stocks. Thus, in the Seto Island Sea, Hirose (1979) found that under conditions of N and P increase due to domestic pollution, G. amansii was one of the surviving species. In San Clemente Island, California, Littler and Murray (1975) found that G. pusillum and P. capillacea were quite abundant in the mid-intertidal area near the outfall of a low-volume domestic sewage discharge. In fact, in this locality these two species had at least doubled their cover-value in the unpolluted control area. Along the Mediterranean coast of Lebanon, P. capillacea was characterized as being able to thrive in nutrient-enriched waters, together with species such as Ulva sp., Enteromorpha sp. and Colpomenia sinuosa (Basson, Hard and Lakkis, 1976). In the North Adriatic, the severe domestic pollution has eliminated many algal species; the previously dominant fucoids are now replaced by associations of nitrophilic species among which the low carpets of Gelidium sp. are quite frequent (Munda, 1981).

A more direct line of evidence has arisen from studies on the effects of fertilizers on beds of Gelidium amansii reported in a series of contributions, by Yamada. He first attempted to find (Yamada, 1961) the form of nitrogen compound that was most effectively used by this species. This was found to be ammonium nitrogen up to 10 ppm. Its uptake was greatly influenced (Yamada, 1964) by the addition of phosphorus. With an optimum concentration of 5 mg (PO_4-P/l, the amount of NH_4-N absorbed was close to 0.5 mg) per gram of wet weight. The optimum ratio of nitrogen to phosphorus was 2 to 1 where the ammonium nitrogen content was 2 to 10 parts per million. Using radioactive phosphorus 32, Yamada et al. (1964) found that phosphorus was rapidly and uniformly absorbed over the whole surface of the thallus.

As a result of these studies, a manure consisting of 8 parts of ammonium nitrogen and 4 parts of phosphate-phosphorus was later proposed (Yamada, 1967) using guano as a binder. In natural populations (Yamada and Iwahashi, 1964), the yellowish thalli of Gelidium became dark-purple in colour within 13 days after manure application. Additionally, there was (Yamada, 1972) an increase in length, weight and nitrogen content of the thalli. The agar content of Gelidium grown in a manured area was slightly higher in both quantity and gel strength than in thalli grown in the untreated areas.

Ammonium nitrogen, however, is not the only type of nitrogen effective in promoting growth in these species. Calabrese and Felicini (1970) grew P. capillacea by the addition of $NaNO_3$ and more recently, Bird (1976), using 4 possible combinations of ammonium nitrogen and nitrate could show that Gelidium nudifrons could simultaneously assimilate pools of both ammonium and nitrate.

Some observational and experimental data tend to indicate that not all the species of Gelidium and Pterocladia might tolerate high levels of nitrogen and phosphorus. In their study on the biological effects produced by the low-volume domestic sewage discharge near Wilson Cove, San Clemente Island, California, Littler and Murray (1975) found that G. robustum had, in the outfall area, a cover value of 1/10 as compared to the unpolluted control area, while G. coulteri was represented only in the control area but absent in the polluted site. More recently, Macler (1983) has reported that nitrogen deprivation resulted in increased growth rates and agar yields of experimentally grown thalli of G. coulteri, G. purpurascens and G. robustum. Agar yields were unaffected by variations in the amount of phosphorus in the culture media.

Little is known about other nutritional requirements of the species of Gelidium and Pterocladia. The only pertinent study found is the demonstration of the effects of carbon dioxide on photosynthesis of Gelidium amansii (Ogata and Matsui, 1965). At 30°C, 10 klux and shaking velocities of 140-150 cycles/minute, the species reached maximum photosynthetic rate at a concentration of 8×10^{-3} M of $NaHCO_3$ per liter. Lower carbonate concentrations decreased the photosynthetic maximum.

2.4.4 Growth

A description of spore germination and further development in the species of Gelidium and Pterocladia have been given in Section 1.2.1.1 of this report. Seasonal variation in spore production and germination patterns are to be found in Section 3.2.

The growth rates frequently measured in these species are a quantitative expression of the rate at which regeneration can occur. Intertidal and subtidal populations of Gelidium and Pterocladia can recolonize the substratum and regenerate new fronds. According to Suto (1974), Okamura reported experiments with regeneration of Gelidium along the coast of Japan as early as 1911. Thalli were cut into small pieces and attached to rocks with palm strings or held beneath rocks. Using the latter method, Okamura observed the formation of rhizoids along the stem of a thallus at the edge of the rock, while the portions of the thalli beneath the rocks had decayed. Some years later, Katada (1955) extensively described both regeneration and the formation of new fronds from creeping axes. He also noticed that when the thallus was attached to a rock, some of the branches could become prostrate and behave as creeping axes able to form new erect fronds.

The time required for the recovery of natural populations by regeneration seems to vary according to specific or habitat differences. On the Monterey Peninsula, California, no recruitment of Gelidium was observed (Northcraft, 1948) in cleared intertidal areas during a two year study. In the intertidal region of Ghana, it took (Lawson, 1966) ten years of Gelidium sp. to reach a cover value similar to that before the clearing of two permanent quadrats. Other species, however, seem to regenerate more easily. Thus, G. latifolium from England developed (Dixon, 1958a) erect fronds during three successive years after they had been removed, leaving only the creeping axes, and Pterocladia capillacea from New Zealand regained its full length (Chapman, 1970) eight months after being cut.

Seasonal variation of the regeneration capacity has also been observed in some populations. Intertidal thalli of Gelidium pusillum from Spain, cut during winter, quickly developed (Seoane-Camba, 1965) underneath the fast growing populations of Ulva and Enteromorpha. Those cut in the spring did not show a rapid recovery and the substratum was invaded by barnacles that were reproducing at that time. For populations cut in the summer, Lyngbya and Oscillatoria were the only species to establish themselves during the first month, followed later by Enteromorpha and Gelidium.

In the case of subtidal populations of Gelidium robustum from California, some periodicity has also been found. The initial regeneration, within the first two months after harvesting, was significantly greater (Barilotti and Silverthorne, 1972) from June to December than from January to May. Intertidal populations, however, did not show such a seasonality (Johnstone and Feeney, 1944) in the production of new shoots.

Field elongation rates of seven species of Gelidium and Pterocladia have been measured in different areas of the world (Table 3), and very characteristically, the measured rates in most species are 9-10 cm/year. Both Barilotti (1980) and Stewart (1984) have called attention to these relatively slow growth rates as compared to other types of algae. Stewart (1984) has suggested that this slow growth rate is an intrinsic feature of these taxa, rather than one that can be manipulated by external physical factors.

Measurements of elongation rates give direct or correlated information on biomass only when the presence of lateral branches is taken into account. Studies of such relationships have been performed in Gelidium robustum in which the laterals elongate at the same time as the main axes (Barilotti and Silverthorne, 1972). Care should be taken, however, in extrapolating results, because in these populations, dry weight as a function of length was found to vary from thallus to thallus. Furthermore, the production of laterals was found to change with time. Initially, the axes do not produce laterals, whereas with time, the older laterals are lost from the main axes.

Specific differences in growth rates obtained under experimental laboratory conditions are abundantly found in the literature. These differences have already been discussed in relation to the effect of environmental factors on growth. It should be noted, however, that specific growth rate values are strongly influenced by the branching pattern of the material under study. In spite of the relatively constant growth rate of 10 cm/year of Gelidium robustum in California, Barilotti (1980) has indicated that a higher growth rate can be achieved if plants have many axes growing. The large the body of the plant (and the higher the number of laterals), the faster the increase in biomass.

The effects of growth promotors such as IAA and some morphoactines such as chlorflurenol have been studied in the closely related genus Gelidiella (Sreenivasa Rao, 1973; Tewari, 1975) but no experiments seem to have been performed with Gelidium or Pterocladia. Calabrese and Stefanizzi (1974) have reported that concentrations of 2×10^{-5} and 2×10^{-6} M of lycorine inhibit growth and pigment formation in Pterocladia capillacea. Lycorine is an alkaloid inhibiting growth and cell expansion in higher plants.

Table 3

Field elongation rates measured in species of Gelidium and Pterocladia

Species	Rate	Place	References
G. crinale	6 cm/year	England	Dixon, 1966
G. robustum	9 cm/year	California, USA	Barilotti and Silverthorne, 1972
G. nudifrons	3-4 cm/year	California, USA	Stewart, 1984
P. lucida	10 cm/year	New Zealand	Luxton, 1977 (fide Stewart, 1984)
P. capillacea	3-15 cm/year	California, USA	
G. amansii	10 cm/year	Japan	Suto, 1974
G. sesquipedale	9 cm/year	Spain, Galicia	Seoane-Camba, 1966
	9.36 cm/year	Spain, Santander	Seoane-Camba, 1969
G. pristoides	8.4 to 9.0 cm/year	South Africa	Carter and Anderson, 1986

3. LIFE HISTORY

3.1 Life Cycle

3.1.1 Alternation of generations

The species of Gelidium and Pterocladia are supposed to have a "Polysiphonia type" of life history with equal proportions of tetrasporic and sexual generations (Kylin, 1923). The occurrence of sexual and tetrasporic phases has been later confirmed in field materials of several species of Gelidium and Pterocladia (Kylin, 1928, 1956; Okamura, 1934; Feldman and Hamel, 1934; Fan, 1961; Stewart, 1968; Oliveira and Sazima, 1973; Santelices, 1977, 1978). At least in P. lucida, erect fronds developed from carpospores produced tetrasporangis after 7-10 months of cultivation (Luxton, 1977).

In spite of this "Polysiphonia type" of life history, many workers in different latitudes have pointed out the conspicuous differences in the proportions of tetrasporangial and sexual thalli (Johnstone and Feeney, 1944; Dixon, 1959a, Yamasaki and Osuga, 1960; Seoane-Camba, 1966; Stewart, 1968; Akatsuka, 1970, 1973; Barilotti and Silverthorne, 1972; Oliveira and Sazima, 1973; Guzmán del Proó and de la Campa de Guzmán, 1979; Montalva and Santelices, 1981). The tetrasporangial thalli are often more frequent or more abundant by several orders of magnitude than sexual thalli. For example, Akatsuka (1973) found only 34 male individuals of Pterocladia capillacea after careful examination of material including over 1 000 individuals collected near the Experimental Station of Tokyo University of Fisheries. Likewise, Guzmán del Proó and de la Campa de Guzmán (1979) found in Gelidium robustum from Baja California a dominance of tetrasporangial thalli throughout the year with a ratio of 12:1 or higher in respect ot gametangial thalli. In G. lingulatum and G. chilense from central Chile, the biomass of sexual thalli throughout the year amounted to less than 10% of the fertile biomass (Montalva and Santelices, 1981) while the bisporophyte generation of G. pristoides dominated over the gametophyte generation by a ratio of about 3:1 (Carter, 1985).

Several hypotheses have been advanced to explain the differences in proportion of sexual and tetrasporic thalli. Dixon (1961) developed life history studies, concluding that a regular "Polysiphonia type" of life history may occur in one of the British species of Gelidium, although he detected some irregularities. For a second species of British Gelidium, the results were so irregular that accurate interpretation of the life history was impossible. In the case of Pterocladia capillacea from England, Dixon (1959a, 1961) found it to be completely sterile during nine years of research. This species, however, is fertile in other areas of Europe (Feldman and Hamel, 1936; Seoane-Camba, 1966) as it is on the Pacific coast of the USA (Stewart, 1968) and on the Hawaiian Islands (Santelices, 1977). Based on his results, Dixon (1961) suggested that local variations in the life history of these species could be considerable, and that meiosis may not be occurring in all sporangia of a given sporophyte. Therefore, the spores resulting from the same thallus may be haploid or diploid which, added to the diploid carpospores, could account for the high field representation of diploid sporophytes.

An alternative view was derived from field transplants of Gelidium amansii performed by Yamasaki and Osuga (1960) in Japan. Populations grown on artificial beds of stones had, during the first or second year, a large proportion of female thalli. The cystocarpic thalli accounted for 33 to 100% of the total population, with a mean of about 64 percent. As the age of the stone bed increased, the proportion of female thalli gradually decreased to 20 to 35% of the population, nearly the same proportion found among those occurring on natural rocks. Assuming that no sampling errors and no drastic changes in other environmental parameters had occurred during the 5 years of these observations, Santelices (1974) suggested that this might be interpreted in terms of intraspecific competition between tetrasporic and sexual thalli. Increased sensitivity to environmental parameters and reduced competitive ability could be expected to occur in the sexual haploid phase, while increased vigor could be expected to occur in the diploid thalli, leading to the possibility of a gradual field replacement of haploid by diploid thalli. Barilotti (1980) has agreed with this hypothesis, although he stressed that up to 1980, no direct survivorship difference has been experimentally tested between both phases nor has evaluation of the importance of reproductive effort leading to diploid dominance been performed in any species of Gelidium and Pterocladia. Recently, Carter (1985) reported that the growth responses of sporophytic and gametophytic germlings of G. pristoides was very much the same under a variety of culture conditions. However, carpospores did germinate more successfully than bispores, a fact that might explain the abundance of diploid plants.

Studies on reproduction patterns of the species of Gelidium and Pterocladia have called attention also to the extended sterility of some species, especially at the extremes of their geographic distribution. As already commented, Dixon (1965) studied the phenomenon in populations of Pterocladia capillacea from Europe. The species is widely distributed, but sterile, in England, Wales and Ireland. No traces of germlings or vegetative propagation were found in several years of research, although individual clones were observed to survive and remain in the same position for many years. According to Dixon, tetrasporic thalli of this species occur southward from southern Finistère (France), and cystocarpic thalli are present still further south in northern Spain. Based on this pattern, shown for several other species of red algae, Dixon (1965) hypothesized that the phenomenon may be explained in terms of physiological expression of some reproductive capacity. Both sexual and tetrasporic thalli are likely to be found in the centre of the distributional areas of the species. Toward the limits of these areas, external conditions would inhibit the expression of the haploid sexual thalli, although the diploid thalli would produce tetraspores. Furthermore, at the limits of their distributional areas, the reproductive potential of both haploid and diploid thalli would be completely inhibited. The establishment of the thalli in these two parts of the distribution area would be by spores, by vegetative propagation or both. This idea was later tested with the tropical species Pterocladia caerulescens, a common member of intertidal and shallow subtidal Hawaiian communities (Santelices, 1978). These populations showed a notorious scarcity of sexual plants. Spermatangial thalli were never found and cystocarpic plants occurred only in June accounting for less than 10% of the wet biomass collected during that month. The complete geographic distribution of P. caerulescens is unknown, but it seems to be essentially tropical as the species has been found under several names (Santelices, 1976a), in the Caribbean (Kutzing, 1968) and in the Tropical Pacific (Dawson, 1959; Loomis, 1960; Santelices, 1976a, 1977). The scarcity of sexual thalli of this species is therefore unexpected in Hawaii and cannot be fully explained by Dixon's hypothesis which supposes similar abundance of haploid and diploid thalli in the geographic centre of the species' distribution area.

3.1.2 Nuclear phases

As indicated previously, few karyological studies have been performed in species of Gelidium and Pterocladia (Magne, 1964; Kaneko, 1966, 1968) while cytological evidence of meiosis during tetraspore formation is lacking for both genera. Such a phenomenon, however, has been found in other genera of the Gelidiaceae. In Acanthopeltis japonica, Kaneko (1968) found that the diploid set of chromosomes (2n = 30) did divide meiotically during spore formation. Likewise, in Gelidiella acerosa belonging to the closely related family Gelidiellaceae, Sreenivasa Rao (1974) found that his counts of 8 chromosomes in vegetative cells was reduced to four in the prophase of the second meiotic division of the tetrasporangium.

3.2 Reproduction

Reproduction has been found to be a seasonal phenomenon in many species of Gelidium and Pterocladia and is generally assumed to be temperature-regulated. Cystocarp formation seems to be connected with optimum growth conditions and therefore, is seasonal in the places where growth is also seasonal. This occurred in Gelidium corneum from the Texas lagoons (Conover, 1964) and in the seven species studied by Matsuura (1958) in Japan. In the cases of Pterocladia capillacea from San Diego, where seasonal growth was not found (Stewart, 1968), cystocarp production occurred during the whole year. A similar situation exists in G. lingulatum and G. chilense (Montalva and Santelices, 1981).

With few exceptions, tetraspore formation has also been shown to be seasonal. Even Pterocladia capillacea from San Diego, where neither seasonal growth nor seasonal cystocarp formation was detected, produced tetraspores (Stewart, 1968) only during the warmest months of the year. So far five species have been found to lack seasonal tetraspore formation. They are G. sesquipedale from Spain (Seoane-Camba, 1965); G. robustum (Barilotti and Silverthorne, 1972), from Baja California; and two species of Gelidium from central Chile (Montalva and Santelices, 1981); and G. pristoides from South Africa (Carter, 1985). The first two species, however, have two other peculiar seasonal aspects of reproduction to be discussed later. Fertility of the two species from central Chile, as discussed previously, is affected by interspecific interference.

The amount of growth or the age required before young thalli can become reproductive is poorly known in these species. Some observations indicate that intertidal individuals of Pterocladia capillacea from San Diego, California, did not develop reproductive structures (Stewart, 1968) during three years of observations, but 2 to 3 year-old intertidal thalli of Gelidium latifolium from England were (Dixon, 1959a) producing tetraspores. In G. pristoides only plants greater than about 30 mm in height possess reproductive structures (Carter, 1985).

The amount of growth required for subsequent reproduction also varies among different species. In subtidal populations of Gelidium robustum from Baja California, tetrasporic thalli were in fruit (Barilotti and Silverthorne, 1972) one year after harvesting; therefore, the authors recommended a growth period of two years in order to allow one season of recruitment. By contrast, in Pterocladia capillacea from San Diego, Stewart (1968) found that differences in position of the reproductive structures indicate that some thalli may produce spores or gametes the first year, but they do not necessarily become fertile every year.

Amounts of spore production per unit of frond and per unit of time are important initial indications of the reproductive potential of a species. Such calculations were done (Suto, 1950a) for Gelidium amansii, which during the shedding season can produce daily 10^4 to 10^6 spores per gram of thallus. G. robustum from Pacific Mexico reached a maximum (Guzmán del Proó, de la Campa de Guzmán and Pineda-Barrera, 1972) of 299 072 carpospores and 27 453 tetraspores per month and per each thallus of about 12.5 to 15 cm. In this last species, tetraspores were produced during most of the year.

Spore shedding is seasonal in many species of Gelidium and Pterocladia. The shedding of both tetraspores and carpospores of G. amansii from Japan was thought (Suto, 1950a) to start when water temperatures rose above 20°C and 24°C, respectively. Subsequent studies confirmed (Katada et al., 1953) a seasonal change in the time of shedding. Time of shedding became gradually earlier in the day from June to September, after which, and up to November, it occurred later in the day. Direct evidence of a temperature influence on spore shedding was later produced by Katada (1955) for several species of Gelidiaceae from Japan, who concluded that the higher the water-temperature is during the preceding night (up to a maximum of 25°C), the earlier the spores of the species are shed. Spore shedding, however, seems to be a phenomenon affected by several other environmental factors as well. In G. pusillum and P. heteroplastos from India, Umamaheswara Rao and Kaliaperumal (1983) showed that desiccation, light intensity, photoperiod, salinity and temperature all affected the process. Thus, spore output declined rapidly up to 30 minutes of air exposure and complete inhibition was seen after 90 minutes of air emersion in G. pusillum and 60 minutes in P. heteroplastos. In both species, maximum spore output occurred around 500 lux, decreased spore output after 1 000 lux and complete inhibition after 4 500-5 500 lux. Spore production occurred within a wide range of salinities (10 to 60°/oo) and temperatures (10 to 40°C) but maximum output in both species was at 30°/oo and 25°C.

Spore dispersal and attachment represent the next important phase after spore production. The mechanism of spore dispersal in most species of Gelidium and Pterocladia remains unknown, but a conspicuous seasonal phenomenon, possibly to be interpreted as a spore-dispersion adaptation has been reported (Seoane-Camba, 1966) for Gelidium sesquipedale from Spain. Field observations indicated that the biomass of cast weeds of this species increased toward autumn. Seoane-Camba found that the percentage of fertile thalli in the cast weed was higher than that occurring in similar attached populations. He also observed that most of the cast seaweeds were apical portions of branches, and that the defoliation does not necessarily mean destruction of the whole thallus. Therefore, he concluded that this phenomenon could, among other adaptative functions, represent a special adaptation for spore dispersion.

In situ studies on the dispersal of juvenile thalli have been made in Gelidium robustum (as G. cartilagineum) from the Pacific coast of Mexico. A circular area of 1 m in diameter was cleaned of vegetation (Guzmán del Proó and de la Campa de Guzmán, 1969), leaving a parent thallus in the centre of the area. After 5 months, there were 41 new thalli in the 1 m diameter area. The maximum number of young thalli was found starting 40 cm from the parent thallus. In the area between the 40 cm and 1 m radius, 40 to 41 new thalli were found. No explanation of the causes of this distribution pattern or estimates of the reproductive potential (spore production) during the experiments were given.

There is some information on sinking and settling of spores of Gelidium amansii. Sedimentation velocities of tetraspores and carpospores were (Suto, 1950, 1950a; Katada, 1955) about 1 mm per 20 seconds. Their fixation capacity is maintained for 2 hours or more while substrate with irregular surfaces shows improved adhesion of spores.

Spore germination has been shown to be influenced by temperature in Gelidium amansii, with maximum germination between 24 and 26°C (Katada, 1949, 1955). Temperature regulation of a seasonal spore germination and growth was also suggested (Barilotti and Silverthorne, 1972) for G. robustum from Baja California. Juvenile thalli, growing on artificial substrata, were observed only in February. Thus, although the species was fertile all year round, only the spores released during the spring and early summer were successful in producing juvenile thalli on new substrate. Laboratory experiments, however, have shown that at temperatures ranging from 10-20°C, three different photoperiodic regimes and photon-flux densities from 25 to 75 $\mu E/m^2/s$ did not induce significant differences in germination values of Gelidium lingulatum and G. chilense from central Chile (Correa, Avila and Santelices, 1985).

3.3 Phenology

As already explained in Section 2.3.2, many species of Gelidium and Pterocladia have annual growth cycles. In England, P. capillacea produces cylindrical axes during spring, which soon stop growing in length but continue growing in breadth. Axes of mature fronds, therefore, are broad and flat but have marks resulting from the early elongation of the axes. Since the erect fronds persist for a number of years, these marks have been suggested to be used to trace longevity of the population. Such a cycle has been described in several other populations of P. capillacea (Dixon, 1963a, 1970), in Gelidium corneum (Conover, 1964) and G. sesquipedale (Seoane-Camba, 1969).

However, more recent studies have uncovered one source of complication limiting the use of morphological changes to trace longevity. This is derived from the evidence that reproductive processes, especially those related to tetraspore formation and shedding, are also responsible for morpho-phenological changes. In Pterocladia caerulescens from Hawaii, main axes elongate from July to December (fall to winter). Tetraspore formation, shedding and apical decay occur following additive growth, thus shortening the axes and reducing the number of branches (Santelices, 1978). A similar phenomenon has been described for Spanish populations of G. spathulatum and G. crinale (Gómez-Garreta, Ribera Siguan and Seoane-Camba, 1982; Echegaray-Taborga and Seoane-Camba, 1982). These populations of G. spathulatum are tetrasporangial throughout the year. However, maximum spore production occurs in summer, after which time there is an apical die-back and reduction in the length of the axes. Perhaps, Oliveira and Sazima (1973) were observing the same process in Brazilian populations of P. capillacea when they described a reduction in the mean size of the plants produced by some sort of abscission of the apical end of erect axes during winter. Also in this case, the die-back of the apical ends occurred in the fall after maximum spore production in the population.

4. POPULATION STRUCTURE AND MORTALITY

4.1 Age, Weight and Size Composition

Because vegetative reproduction is common in species of Gelidium and Pterocladia, the basalmost portion of erect axes as well as the creeping axes might be several years old. Therefore, age composition can be studied only in natural populations of erect axes.

Since the growth of most species of Gelidium and Pterocladia is apparently less than 10 cm per year, and since some species are large than 30 or 40 cm, it has been concluded (Seoane-Camba, 1966; Barilotti and Silverthorne, 1972) that such species live more than one year. Field studies have confirmed this idea and have also shown habitat-related differences in longevity. In the case of Gelidium latifolium and G. crinale from England, Dixon (1966) found that the subtidal fronds persist for 2 to 3 years, while those occurring higher in the intertidal zones are annually produced in the spring. In the case of Pterocladia capillacea, subtidal erect fronds could persist for up to 5 years. Similar habitat-related differences exist in the Hawaiian populations of P. caerulescens (Santelices, 1978) and they are probably widespread among species of Gelidium and Pterocladia.

More accurate estimates of age composition have been performed in the Spanish populations of Gelidium sesquipedale. The seasonal apical elongation and branch production leave marks on the plant forming true lines of growth (Seoane-Camba, 1969). If these line are connected, it is possible to divide the plant in bands or layers whose height can be measured and the biomass weighed. Using these reference points, Seoane-Camba (1969) thought that he could determine elongation patterns as well as production and losses of biomass, and make estimates of age of erect axes in G. sesquipedale. It should be noticed however, that the method cannot be applied to species lacking a seasonal pattern of growth or to ecological situations where growth lines can be confused with frond marks from a different origin (e.g., grazing).

Since no accurate estimates of age can be done in most natural populations of species of Gelidium and Pterocladia, an approximate description of the structure of these populations has been obtained from the size distribution of fronds. A careful methodology was developed in the Californian populations of G. robustum by Silverthorne (1977) which allowed the estimation of several population parameters. First, the continuous range of possible frond lengths was divided into intervals with all the fronds falling in a particular interval being treated as if they were at the mid-point of that interval. In order to determine the proper intervals for the size-classes, Silverthorne (1977) determined the average elongation per quarter. This was performed by photographic recording of elongation rates of individual fronds over six intervals throughout a period of approximately a year. The average rate determined was 2.25 cm/quarter. Theoretically, the first size class should be formed by fronds recruited into that class during the previous period. Therefore, they should be less than 2.25 cm in length. However, it was found to be too difficult to measure, count or otherwise collect data on fronds this small while working underwater. Therefore, Silverthorne (1977) decided to treat the first 2.25 cm of the frond as part of the holdfast. Thus, the first size-class included all fronds from 2.25 to 4.51 cm. Recruitment was defined as the entry of new fronds into this size class, and biomass was considered as the weight of the frond, excluding the first 2.25 cm.

Since the population structure is affected by survival rates, survival rates for each period of study (four quarters) were obtained from tagged plants in the field. The computed survival rates averaged about 0.6, which was considered to be too low to support the luxuriant Gelidium growth at the study site. In order to reach a more realistic estimate of the loss rate, a square meter of Gelidium bed near one of the study sites was harvested. Then, the fronds were assigned to size classes and the appearance of population distribution analysed. This suggested a seasonal pattern superimposed on a negative exponential function, as would be expected (Silverthorne, 1977) from a population subjected to seasonal fluctuations in recruitment of new fronds and with exponential loss rate. By calculating loss rate for each size class in the population, Silverthorne concluded that the loss rate (L.R.) of the population was a function of frond length (L) under the expression LR = -0.00307 L, with a sample correlation coefficient of -0.989. With these data it was possible to recalculate loss rates for the various size-classes, evaluate the seasonal variations in loss rates and calculate survival rates for different frond sizes.

Average weight of fronds in each size-class were also obtained from the fronds removed from the meter quadrate. The power function $w = AL^x$ was then fitted to these data, the resulting equation being $w = 0.00159\ L^{2.0033}$ where w is the weight in grams and L is the length in centimeters (r [1/] = 0.93385).

Regeneration and recruitment for the first quarter following harvesting of G. robustum were estimated experimentally. At different times of the year, all axes of transplanted clumps of G. robustum were trimmed to within 2 cm of the holdfasts. After two months, all axes over 2 cm were counted and the number of regenerated axes noted. All viable fronds over 2 cm in length were taken to be recruits. Since spore germination in this species is seasonal (Barilotti and Silverthorne, 1972), most of the recruits were cut fronds which had regenerated their apical meristem. Data suggested a seasonal pattern of recruitment, with an increase in winter and fall. Knowing the dry weight biomass harvested per square meter, and the size-class distribution, Silverthorne (1977) could then calculate the average number of recruits, which was 145.65 fronds per quarter. This approximation probably could be used elsewhere in populations of these algal species.

Population structure based on weight and size composition has also been studied in Gelidium sesquipedale near Santander, northern Spain (Salinas, Ramírez and Olivet, 1976; Reguera, Salinas and Gancedo, 1978). The rhizoids of this species grew new stems constantly, and some of the erect axes were found to be at least 6 years old. The potential yield of a Gelidium bed was found to depend heavily on regeneration of erect axes rather than on spore germination. Axis trimming and regeneration depended on local factors such as wave impact and grazing; therefore, different seaweed beds had different size distribution patterns.

4.2 Sporophyte - Gametophyte and Sex Composition

Biological findings and interpretations dealing with the notorious sterility of populations of Gelidium and Pterocladia as well as discussions related to the abundance of tetrasporangial thalli over sexual plants have been reviewed in Section 3.1.1.

1/ r = sample correction coefficient

4.3 Density

Since it is often impossible to distinguish individuals of Gelidium or Pterocladia, density measurements are infrequently used in ecological studies of these species. Measurements of fresh or dry weight per unit area have been defined as density in some reports. Such information is included in Section 5 under standing stock values.

4.4 Mortality - Morbidity

Water movement has been observed to extensively destroy the wild crop of Gelidiaceae. The weeds cast on the shores of New Zealand and Spain are a good illustration of this phenomenon. In Baja California, mechanical breakage of the axes of intertidal populations of Gelidium robustum was observed (Johnstone and Feeney, 1944) to be more abundant in spring and fall when water movement was stronger. In subtidal populations of this same species, the losses of thalli were related (Barilotti and Silverthorne, 1972) to length of the axes and the seasons, the losses being greater for longer axes in winter. On the Azores, hydrodynamic fragmentation of Pterocladia capillacea was observed at least during three months in a year (Fralick and Andrade, 1981). The fragmentation process apparently had no physiological basis but consistently occurred during storms. Plants longer than 10 cm seemed particularly sensitive to storm-induced wave damage (Fralick and Andrade, 1981).

Intense radiation coupled with high temperatures can produce bleaching and destruction of intertidal populations during day-time low tides, and may produce bleaching and decreased growth of subtidal populations toward the end of the summer. The ecological factors involved in this last type of phenomenon have been discussed in Section 2.3.1.

Grazing by invertebrates and fishes is also expected to cause extended mortality in populations of Gelidium and Pterocladia and even interact with water movement, trimming the longer axes. This is the case of subtidal populations of G. sesquipedale from Santander in northern Spain. Invertebrates feeding on these species cut and sever stems especially 2-4 cm above the holdfast. Some thalli however, are bitten but not cut by grazers. Increased water movement can then accelerate their removal. As the axes grow, they escape from invertebrate grazing but are more likely to be cut by fishes (Salinas, Ramírez and Olivet, 1976; Reguera, Salinas and Gancedo, 1978).

It should be noticed, however, that the above examples of mortality imply destruction of erect axes and not necessarily of the whole plant. In most of these populations, new branch apices generate from the rhizoidal portions of plants in a matter of days or weeks (Barilotti and Silverthorne, 1972; Reguera, Salinas and Gancedo, 1978; Fralick and Andrade, 1981).

A longer-lasting sort of mortality is the one produced by careless harvesting with removal of creeping axes. As will be discussed in Section 6.1, this is a serious problem in several areas of the world which reduces the regeneration capacity of commercial beds.

Consumption of spores and embryos by invertebrate grazers is a factor likely to cause extended mortality, especially in intertidal habitats. However, only Jernakoss (1983) seems to have obtained some quantitative data for G. pusillum. Likewise, the commonly described parasites and epiphytes found on thalli of Gelidium and Pterocladia perhaps increase mortality of some host species, but scarcely any field observations exist on this subject.

5. PRODUCTIVITY OF THE RESOURCE

5.1 Standing Stock Values of Wild Resources

Species of Gelidium and Pterocladia are among the most important agarophytes in the world, and a few species are also consumed as food by indigenous people. Over 35 species of Gelidium and Pterocladia are collected for agar extraction in several areas of the world (Table 4) and stocks and production values are available for some of them.

The quantities of annual production of Gelidium and Pterocladia reported by Yamada (1976) are summarized in Table 5. They range between a minimum of 15 000 and a maximum of 19 000 dry tons per year. It should be noticed that Yamada (1976) did not include in his list 1 000 to 1 500 tons of P. capillacea annually harvested on the Alexandria coast, 300 tons of Gelidium annually collected in Madagascar and 50 to 60 tons of G. pristoides gathered in South Africa (Michanek, 1975; Carter and Anderson, 1986). Thus, the amount of species of these two genera used annually in the production of agar might be slightly over 20 000 metric tons. In some areas such as Japan, the materials identified under the name of Gelidium might also include other genera in the family such as Beckerella, Suhria and Yatabella and in Indonesia, they might include Gelidiella acerosa. However, in most of other places, these values strictly correspond to species of Gelidium and Pterocladia.

Table 4

Species of Gelidium and Pterocladia used as raw material for agar production

Species	Place	Fishing area number
G. amansii	Japan, China	61
arborescens	USA	77
attenuatum	Japan, China	61
arbuscula	Canary Islands	34
cartilagineum	Canary Islands, South Africa	34
caulacantheum	New Zealand	81
chilense (= filicinum)	Chile	87
corneum	Spain, Portugal, Morocco	27, 34
coulteri	USA, Mexico	77
crinale	Japan, Gulf of Guinea	61
densum	Southern California, USA	77
divaricatum	China, Japan	61
elegans	Japan	61
japonicum	Japan, Korea, Taiwan (Prov. of China)	61
latifolium	Japan, China, Indonesia	61, 71
lingulatum	Chile	87
linoides	Japan, Korea, China	61
nudidrons	Japan	61
pacificum	Japan, Korea, China	61
planiusculum	Japan	61
pristoides	South Africa	34
pulchellum	Ireland	27
pusillum	Pakistan, India	51, 57
rex	Chile	87
robustum	Mexico	77
serrulatum	Venezuela	31
sesquipedale	Spain	27
spinulosum	Morocco	34
subcostatum	Japan, Korea, Formosa	61
subfastigiatum	Japan	61
tenue	Japan	61
vagum	Japan	61

Table 4 (cont'd)

Species	Place	Fishing area number
Pterocladia capillacea (including densa, nana, pinnata, tenuis)	Japan, New Zealand, Egypt, Northern Brazil, USA	61, 81, 37, 41, 77
heteroplastos	India	51
lucida	Australia, Tasmania, New Zealand	81, 57

Table 5

Annual crops of Gelidium and Pterocladia harvested in different areas

Place	Fishing area number	Metric tons (dry)	Harvesting method used
Spain	27	4 000 - 5 500	Drift, trawling and diving
Japan	61	3 000 - 3 300	Hand picking, diving
Portugal	27	2 500 - 3 000	Drift, hand picking
R. Korea	61	2 000 - 2 500	Hand picking
Mexico	77	1 000 - 1 500	Diving
Morocco	34	1 000 - 1 500	Hand picking, drift
Indonesia	71	400 - 500	Hand picking
France	27	300 - 400	Drift
USA	77	150 - 200	Diving, hand picking
Chile	87	100 - 150	Hand picking
P.R. China	61	100 - 150	Hand picking
Korea DPR	61	80 - 100	Hand picking
New Zealand	81	50 - 100	Hand picking
Taiwan (Prov. of China)	61	50 - 60	Hand picking
Total		14 730 - 18 960	

The standing stock values normally found in commercial beds vary widely from a few hundred grams to a maximum of 1.5 kg/m^2. In Japan, the fishing fields are classified as excellent if the standing stock is above 1.5 kg/m^2; good if the stock is between 1.0 and 1.5 kg/m^2; common or normal if the biomass of Gelidium is between 0.5 and 1.0 kg/m^2, and bad if the value is less than 0.5 kg/m^2 (Okasaki, 1971). The commercial beds of G. pusillum and Pterocladia heteroplastos from India normally have stocks of 0.5 to 1.3 kg/m^2 (Kaliaperumal and Umamaheswara Rao, 1981) while the subtidal beds of G. robustum in Pacific Mexico have stocks of the order of 1.08 to 2.06 kg/m^2. Most other Gelidium fields however, seem to approach the values of 0.15-0.2 kg/m^2 recorded for G. coulteri from the Californian coast (Hansen, 1980) and perhaps less. Only the high price of these algae allows commercial exploitation of beds with standing stock values below 0.5 kg/m^2. These high economic returns seemingly have motivated intensive exploitation of the best known beds of Pterocladia and Gelidium at present. This literature survey did not find evidence of any known

productive beds lacking present exploitation except those in highly developed areas such as the USA and Europe where human labour is so expensive that fishing activities are only concentrated on resources of very high economic value.

5.2 Factors Affecting Productivity

5.2.1 Wild resources

Sections 2.3 and 4.3 have reviewed the effects of various ecological factors on the growth and production of these species and the most frequent causes of mortality in natural populations. As already stated, much of this information has been obtained from field observations of population changes correlated with variations in ecological factors, or from laboratory experiments. Much more infrequently, the problem has been approached from the perspective of crop production, and essentially there is no quantitative information on the environmental control of crop production of these species. Numerous, mostly qualitative comments in the literature indicate the following factors as seriously affecting natural production of these wild crops.

(a) Currents: It is widely recognized that the temperature regime and the nutrient contents of some bodies of water could be important in determining the distribution and production of these species. In Japan, it is known that species of Gelidium are common everywhere but they are abundant enough for commercial exploitation only in the Izu Peninsula and the Izu Islands. These areas are influenced by warm water currents (Suto, 1974). Likewise, Guzmán del Proó and de la Campa de Guzmán (1979) have indicated that the most abundant beds of G. robustum along the coast of Baja California are associated with upwelling areas.

(b) Extreme low tides: This represents a widespread detrimental interaction of factors significantly reducing the standing stock values of intertidal crops. For example, populations of Gelidium coulteri in the area of Monterey county, California, are perennial, with a significant seasonal variation in biomass, mainly caused (Hansen, 1983) by a notorious decrease in spring. This biomass reduction immediately follows the extreme low tides during clear daylight hours and results in apparent fatal desiccation. A similar phenomenon has been described in many intertidal populations around the world (Santelices, 1974; Montalva and Santelices, 1981).

(c) Multiple interaction between light, temperature, water movement and nutrients: This multiple interaction is probably a major factor determining the fertility of any given site for species of Gelidium and Pterocladia. As discussed in Section 2.3.1, light intensity and temperature stimulate growth in many species but at high levels, they produce pigment destruction and bleaching. The effects of high light and temperature can be counteracted by increasing the nutrient supply. This can be achieved by increasing water movement or adding nutrients to the culture medium (Santelices, 1977). Natural, commercial crops of Gelidium amansii in Japan have been treated with artificial fertilizers to obtain recovery of the beds from the bleaching effects of high light and higher temperature at the end of the summer (Yamada, 1972, 1976). By the addition of a manure containing ammonium nitrogen and phosphorus, Yamada (1976) obtained an increase in pigment concentration in the thalli of the treated populations within 13 days after treatment. Thallus elongation in the treated thalli was significantly higher than in the untreated control specimens. Biomass production in the manured area increased to about double the value found in the control plots.

(d) Water movement: As commented in Section 4.4., storminess has been reported to remove the longer (and probably heavier) axes in populations of Gelidium robustum from Baja California, G. sesquipedale from Spain, Pterocladia lucida from New Zealand and P. capillacea from the Azores, New Zealand and Alexandria.

(e) Grazing: The effects of fish and invertebrate grazing on crops of Gelidium and Pterocladia have already been discussed in Section 4.4.

(f) Competition: As commented in Section 2.3, studies on interspecific competitive interactions of species of Gelidium or Pterocladia are extremely scarce. The limited information suggests that once established, populations of these species are quite resistant to invasions by other algal species. This is probably due to the occurrence of creeping axes which, especially on substratum with calcareous algae, can survive and produce new erect fronds after harvesting or grazing. In some areas, however, it is quite possible that the bed can be invaded by fast-growing weeds likely to decrease the final value of the commercial crop. In Japan, during the month of April, fishermen spend some time weeding the Gelidium beds and protecting them from invasions, especially of species of Sargassum (Yamada, 1976).

(g) Epiphytes and parasites: The literature does not contain quantitative information on the effects that organisms living on the thalli of Gelidium and Pterocladia might have on their productivity, although there are comments such as those by Guzmán del Proó and de la Campa de Guzmán (1979) indicating that Bryozoa are common epiphytes on about 70% of the thalli of G. robustum harvested in Baja California.

(h) Harvesting practices: Even though these are not natural factors, harvesting practices can have notorious and long-lasting effects on the productivity of Gelidium and Pterocladia beds. Comparative studies of harvesting methods have been performed on beds of Gelidium sesquipedale in Spain (Seoane-Camba, 1966), in populations of G. robustum from Baja California (Guzmán del Proó and de la Campa de Guzmán, 1969) and in populations of Pterocladia capillacea in Ubatuba, Brazil (Oliveira and Sazima, 1973). Generally, the effects of cutting the weed with scissors, pulling the weed from the substratum and scraping the substratum have been compared. Cutting with scissors always resulted in the fastest regrowth, while scraping of the substratum was always the most damaging method, probably due to destruction of the creeping axes. Frequently, the scraped quadrates were invaded by other algae and the original cover or biomass values could not be recovered in the experimental plots even several years after the experiment.

5.2.2 Cultured stocks

Massive cultivation of species of Gelidium and Pterocladia is as yet at the experimental stage with a few laboratory and field attempts performed in different areas. Three basic types of culturing have been attempted.

Field cultivation has been attempted starting either from spores or from vegetative tissues. Spore cultivation of Gelidium amansii in Japan has been performed, modifying slightly the cultivation techniques of microscopic stages of Undaria and Laminaria (Suto, 1983). However, spores take about two years to grow and reach harvestable size (Suto, 1974). More recently, Correa, Avila and Santelices, (1985), were able to define optimal conditions for increased sporeling growth of G. chilense and G. lingulatum but they have not yet entered the stage of field cultivation. Likewise, the efforts to cultivate sporelings of Chinese populations of G. amansii are at a somewhat similar stage of development (Huang, 1982).

Japanese scientists seemingly were the first to attempt field cultivation starting from vegetative branches. They simply attached branches of these algae to a rope which was hung into the sea. Plants grew quite well (Suto, 1974). However, the economic cost of the plants used as seed and the cost of the labour force needed for setting the seed plants to the ropes were so high that the whole operation left little profit. This same type of field culture is being attempted in California with Gelidium robustum and G. nudifrons (Wheeler, Neushul and Harper, 1981). Growth rates reported vary seasonally and range from 0.4 to 2.2% daily. Upwelling events in the cultivation area have been recognized to be quite important in these experiments, by way of increasing the growth rates.

More recently, Friedlander and Lipkin (1982) have reported growing Pterocladia capillacea in string cultures and in floating polyprophylene net baskets of 1 m^2 surface area and 25-50 cm depth, attached to sandy bottoms not deeper than 1 m. In the baskets, P. capillacea showed maximum biweekly growth rates of about 100% while in the string cultures the maximum biweekly growth rate was of 207% during June. Friedlander and Lipkin (1982) noticed that the growth rate fluctuations of P. capillacea did not show any clear correlation with changes in light intensity, temperature or salinity. Perhaps, the authors concluded, other ecological factors such as nutrients may be responsible for variations in growth rate.

The attempts to grow these species under free-floating conditions represent an alternative approach. While working with Hawaiian populations of Pterocladia caerulescens and P. capillacea, Santelices (1976) evaluated the growth of unattached specimens as well as the minimum water volume requirements per unit of algal mass. P. caerulescens and P. capillacea grew continously for 50 days, reaching maximum daily growth rates of 2.3 and 1.6% respectively. Both of these species adopted a globose or subglobose habit, showing modifications similar to other free-floating species of algae. More recently, Mairh and Sreenivasa Rao (1978) and Ruesness and Tanager (1984) have been able to grow Gelidium pusillum from India and Gelidium sp. from Norway under free-floating conditions. Gelidium sp. could reach up to 6.5% of daily growth rate. Light intensity, temperature and photoperiod, were all important in the growth of this species.

Since some species of Gelidium can grow under free-floating conditions, their tank cultivation appears possible. Using G. coulteri from the Monterey area, California, Hansen (1980, 1983) succeeded in growing this species, finding that stocking densities were a significant factor. A specific growth rate of 2.5% per day could be expected from initial stocking densities between 2-3 kg wet weight/m^2. Higher stocking densities produced much lower growth rates while the opposite was true for low stocking densities. The maximum growth rate (6.8%) was obtained at stocking densities of about 1 kg/m^2, but total production was low, only 5 g dry weight/m^2/day as compared to the 17 g dry weight/m^2 produced under densities of 2-3 kg wet weight/m^2.

A completely different approach to Gelidium cultivation has been developed by Gibor et al., (1981). They commented that in 1974, a Japanese patent was issued to the Kureka Chemical Company for a method of agar production employing in vitro callus cultures of algae such as Gelidium and

Gracilaria. The method consists of inducing callus growth by incubation of small pieces of Gelidium thallus at 15°C on an agar medium containing 2 mg/l of the indol acetic acid (IAA), and 0.2 mg/l of kinetins. The medium also contains sucrose, ammonium nitrate, coconut milk, yeast extract, metal ion sulphate and sea water. Pieces of callus are transferred to fresh medium, and it is claimed that they increase in mass eleven-fold in twenty days. The callus tissue was processed and found to yield high amounts of good quality agar. By the use of appropriate procedures to remove epiphytes, (Polne, Gibor and Neushul, 1980), germicides, sterilizing treatments and sterility tests, Gibor et al. (1981), reported having succeeded in obtaining sterile tissues from Gelidium nudifrons.

5.3 Possibilities of Genetic Improvement

No attempts seem to have been made to genetically improve commercial beds of Gelidium or Pterocladia.

5.4 Relative Contribution of Sexual Reproduction and Vegetative Regeneration to the Economic Harvest

As has been extensively commented in several sections of this report, species of Gelidium and Pterocladia are peculiar in their extended sterility, the seemingly strict seasonal regulation of spore production, shedding and germination, and the capacity of creeping axes to regenerate erect fronds. Even commercial propagation of new beds is based on the regeneration capacity of axes. Most of the production of these species comes from vegetative regeneration and growth, after cutting of erect axes, rather than from sexual reproduction.

5.5 Possibilities of Improvement by Environmental Enhancement

So far, the only improvements in production of species of Gelidium and Pterocladia practised by environmental enhancement correspond to the already commented additions of fertilizers in beds of Gelidium amansii in Japan (Section 5.2) and the building of artificial Gelidium beds. These have been achieved by setting stones in areas of potential growth for Gelidium but where substratum is a limiting factor. This is a recommended procedure in areas where productivity is above 0.5 t/ha^{-1}/year^{-1} because expenditures can be recovered in 4 years (see also Section 8.1).

6. HARVEST METHODS

6.1 Annual Cycle of Operations

All of the present harvesting of species of Gelidium and Pterocladia is done from wild crops. Most of the agronomic studies so far performed are therefore oriented toward improving the usage of wild crops and to protecting the crop as a natural resource.

A survey of the practices used to collect the thalli indicate that three practices are in general usage:

(a) Hand-collecting of weeds cast on the shores, especially after local storms;

(b) Hand-picking of intertidal thalli during low tides, or snorkel-collecting in shallow water;

(c) Diver-harvesting from air hose or compressed-air equipped boats in deeper waters.

In Japan, two additional methods are used (Yamada, 1976). Dredging from a boat (1-3 m deep) is performed, while the operator looks through a glass. Alternatively, up to 10 wooden frames with bamboo teeth can be towed from a boat collecting weeds at 20-30 m depth.

In the case of seaweeds cast ashore, it is impossible to control the amount of the material involved, and the collection on the shore has to be done rapidly before the incoming tide disperses the algae, or before the seaweed becomes damaged by exposure to air (Seoane-Camba, 1965; Boney, 1965). Important amounts of this type of material occur (Boney, 1965) in the North Island of New Zealand and in Spain (Seoane-Camba, 1965). Extensive hand-picking of species of Gelidium and Pterocladia from rocky intertidal habitats is practised in South Africa (Isaac and Molteno, 1953, 1953a), New Zealand (Chapman, 1970), Spain and the Azores (Seoane-Camba, 1965; Fralick and Andrade, 1981), Chile (Santelices, Oliger and Montalva, 1981) and Japan (Yamada, 1976). Subtidal hand-collecting by divers is done on the Pacific coast of Mexico (Guzmán del Proó, 1969), the Azores and Portugal (Fralick and Andrade, 1981), Spain (Seoane-Camba, 1966) and Japan (Yamada, 1976). Hand-picking of the thalli is an activity which allows regulation of the subsequent handling and drying and yields agar of better quality.

An annual cycle of operations in harvesting activities of species of Gelidium and Pterocladia is enforced at least in Portugal and Japan. In Portugal, collection of seaweeds fixed to the substratum is by legal regulation restricted to the second half of the year after completion of the population's annual cycle of growth and reproduction (between January and March, Michanek, 1975). In Japan, the fishing season is also limited to a few months (April to October) after the seasonal growth of these populations has been completed (Okasaki, 1971). Since many of the species of Gelidium and Pterocladia occur in habitats exposed to strong water movement, and since storminess in many places displays a seasonal cycle, a naturally closed season probably exists in most areas with commercially important crops.

6.2 Manpower Productivity

The harvesting operations of species of Gelidium and Pterocladia seemingly are so simple that few descriptions related to manpower productivity could be found. Perhaps the most complete assessments are those reported for the harvesting operations in Japan and most of the data refer to yield per unit effort.

As explained previously, at least five different harvesting methods are used in Japan to collect species of Gelidium. One such method is hand-picking seaweeds at depths of up to 15 m after diving from a boat. Divers can stay under the water between 40-60 seconds without breathing and the number of daily hours of work range from 3-6, depending on the sex of the seaweed collector (women can stay in the water about twice as long as men). The estimated catch per diver per day with this method is 40-75 kg of dry matter. This compares well with the 14-16 kg per diver per day estimated to be gathered by fishermen swimming and diving in shallower waters without support from a boat (5-6 m deep). The value, however, is significantly lower than the 60-115 kg gathered by fishermen working on boats and using woody frames with bamboo teeth for harvesting (Yamada, 1976; Cuyvers, 1978). These values can be significantly increased if the season is opened later in the year, or if harvesting is discontinued for two months in the middle of the season (Suto, 1983).

Regarding harvesting in intertidal habitats, the only pertinent data found are those of Kirby (1950), indicating that in New Zealand, a good collector at one tide in a good place could gather an amount equivalent to 25-35 kg of dry Pterocladia lucida.

6.3 Alternate Employment

No information related to additional forms of livelihood of fishermen was found. In Chile, and probably elsewhere, they work gathering other types of seaweed or shellfish during the closed seasons.

7. EQUIPMENT USED FOR HARVESTING AND CULTURE

7.1 Wild Resources

Everywhere the commonest and simplest equipment used in harvesting species of Gelidium and Pterocladia is a net hanging from a float where the collector puts the thalli hand-picked at differeent depths. In addition, Okasaki (1971) has illustrated several other harvesting tools, basically variations of wood frames with bamboo teeth used to scrape the rocks and tear loose the thalli. Then, by the use of trawling nets, the loose materials are collected. Although Okasaki (1971) recognizes that these different materials have different costs, no detailed information on capital and operational costs were provided. Neither were there indications of efficiency of harvesting gear, percentage of the crop retained by the gear or manpower requirements. Seemingly, the few instruments used are all based on the powerful capacity of regeneration and recovery of the species of Gelidium and Pterocladia as they principally trim erect axes.

7.2 Seaweed Culture

Not a single species of Gelidium or Pterocladia is as yet cultivated on a commercial scale. The outcome of laboratory experiments and field attempts to grow them have been summarized in Section 5.

8. PROTECTION AND MANAGEMENT

8.1 Management

Ideally a comprehensive management model should precede intensive harvesting and exploitation of a natural resource. Based on biological, economic, sociological and legal information, a management model can be formulated including, at least, management regulations and enforcements, collector instructions, continued evaluation of the management model and frequent consultation between harvesters, management authorities and biologists. Few studies of this kind have been

attempted for any benthic algae, and they are very rare for the species of Gelidium and Pterocladia. The most thoroughly known examples are the management practices developed in the Japanese beds of Gelidium and Pterocladia. Fishermen's cooperatives are here responsible for the management of the fishery. They select the areas and the days at which harvesting can take place in order to prevent overfishing which could quickly destroy the crop. The cooperatives also regulate the depths at which different harvesting methods can be used. The fishermen sell their daily harvest to the fishermen's cooperative which keeps track of each individual's share and makes cash payment at the end of the year (Cuyvers, 1978). Through biologically-based studies, the various cooperatives have developed management practices aimed at improving crops. They include (Yamada, 1976):

(a) Weeding: In the most productive area of Japan (Izu Peninsula), weeding during the month of April prevents occasional invasions of Sargassum.

(b) Transplantation: Fertile fronds of different species have been transplanted to several different areas in order to increase production. Results (Yamada, 1976), however, have been inconclusive.

(c) Building of artificial Gelidium beds: Natural stones of 20-100 kg have been used, although more recently, tetrahedral concrete blocks have replaced the stones. Growth (elongation) rates measured are of 10 cm per year or 20 cm in 2 years. The cost of artificial beds is recovered in four years in areas where the annual production is about 1-2 kg/m^2. Artificial beds are not economic where Gelidium grows at a rate of 0.3-0.4 kg/m^2.

(d) Regulation of harvesting: As explained above, this includes time and space for harvesting.

(e) Fertilizing: After biological experimentation, a fertilizer was produced, consisting of 8 parts of ammonium nitrogen and 4 parts of phosphate. Its application increases pigment concentration in species of Gelidium, accelerates thallus elongation, increases production to about double, and produces a slight increase in agar content (Yamada, 1976). Its utilization, however, is not yet economic on a commercial scale.

A comprehensive approach to harvesting has been attempted in the California populations of Gelidium robustum. Barilotti and Silverthorne (1972) first estimated the seasonal variation in commercial value of the weed as determined from variations in biomass and agar content. They further studied seasonality of phenomena such as regeneration of harvested axes, and periodicity of reproduction, including both spore attachment and spore production. By integrating all of the above data, they determined the optimum time for harvesting of the species. The optimum period was found to be from August to November, when the agar content was maximum, reproduction had already occurred, and regeneration was at its highest. Since the thalli produce propagules one year after harvesting, a period of two years should be allowed for recovery of a population before the next harvesting.

Based on biological information, Silverthorne (1977) later developed a computer simulation of a Gelidium population as described in Section 4.1 of this report. Then, he calculated revenue function and cost function of the harvesting procedure. With all this information, he developed a model of optimal harvesting policy which was later validated through sensitivity analysis. Through computer simulation, Silverthorne (1977) could evaluate also the impact produced by the harvesting policy if a few parameters were changed. For example, production increases could be obtained by decreasing mortality (frond losses), by making recruitment independent of season, or by increasing elongation rates or frond loss rates. This sort of approach not only allows definition of an optimum harvesting policy, but also gives information as to the relative importance different types of biological information would have on management models. Silverthorne (1977) recommended that future research on population of Gelidium should first concentrate on factors which have the greatest bearing on whether or not any harvest policy is feasible. This sort of biological data would include frond elongation rates, relation of loss rates to frond length, form of recruitment, and seasonal variation in agar content. Once these factors are known well enough for establishing the feasibility, or near-possibility of harvesting the population, then the emphasis should shift to the factors which have been shown to be dominant in determining optimal time of harvesting' elongation rates and seasonal variation of harvesting efficiency.

Apparently unaware of Silverthorne's recommendation, Fralick and Andrade (1981) proposed an apparently empirically determined maximum-sustainable yield of 2 000 t of dried Pterocladia capillacea (as P. pinnata) as annual production in the Azores. They suggested that if the 2 000 t of maximum sustainable yield (MSY) could be maintained for three consecutive years, the MSY could then be increased by 10% for the fourth year. If the annual harvest cannot be maintained at MSY levels, with an equal collecting effort, for two consecutive years, the MSY should be reduced by 10% the third year. Although Fralick and Andrade (1981) measured some biological phenomena such as growth and reproduction in these populations, it was not evident how these biological factors determined an annual MSY of 2 000 metric tons.

8.2 Regulatory Measures

The species of Gelidium and Pterocladia used in industry come from many different countries. Therefore, an analysis of the existing legislation and regulations governing the culture and harvesting of these seaweeds in each of these countries is beyond the scope of this review.

9. UTILIZATION

9.1 Chemical and Nutritional Content

According to Zaneveld (1955), various species of Gelidium analysed by Matsui in 1916 yielded, on a dry weight basis, 2.01% nitrogen, 12.5% crude proteins, 23.7% galactan, 2.03% pentosan, 23.20% reducing sugars; 0.93% methyl pentosan, 17.89% fibre, 0.52% magnesia, 0.28% lime and 4.23% ash. Later studies have reported a protein content of 15.3% in G. amansii and G. latifolium, and a diversity of amino-acids and low molecular weight carbohydrates in G. latifolium and P. capillacea (Johnston, 1966; Impellizzeri et al., 1975); high vitamin B_{12} in several species of Gelidium (Tsuda, Agaki and Kishida, 1958; Güven, Güler and Yucel, 1976; Güven and Güler, 1979); cholesterol and a series of sterols in several species of Gelidium and Pterocladia capillacea (Tsuda, Agaki and Kishida, 1958; Güven and Güler, 1979; Fattorusso et al., 1975; Chardon-Loriaux, Morisaki and Ikekawa, 1976); essential oils with antibacterial and antifungal activities (Güven and Güler, 1979a; Ma and Tai, 1984); and several proteins with lipolytic, hypoglycemic and anticoagulant activities (Güven and Güler, 1979a). The lipid-soluble extract of G. glandulaefolium has been found to have anti-inflamatory properties (Baker, 1984).

The calorific content of species of Gelidium is about 5 kcal per ash-free gram of dry weight (Paine and Vadas, 1969; Littler and Littler, 1980), a value slightly higher than the 4.7 kcal found as average among the Rhodophyta (Paine and Vadas, 1969).

It is interesting to notice that some seasonal variation is expected in the chemical composition of these species. The ash content of Pterocladia capillacea from the coast of Alexandría was maximum in November and minimum in August and was always characterized by a high Ca/Mg ratio (Abdel-Fattah, Abed and Edrees, 1973). Crude protein content also changed seasonally from a maximum of 34.9% in May to a minimum of 11.32% in February. Even the lipid content, which constituted a minor component in the algae had a seasonal pattern of change from a maximum of 1.3% in February to a minimum of 0.6% in November.

9.2 Human Food

Human consumption of Gelidium is restricted mainly to G. divaricatum in China and to G. amansii in Japan, Indonesia, China, and throughout the island of Borneo (Zaneveld, 1955, 1959; Johnston, 1966; Levring, Hoppe and Schmid, 1969). Two other species, G. rigens and G. rigidum are also consumed in these areas, but they probably correspond to Gelidiella acerosa.

Most of the consumption of Gelidium as human food is restricted (Michanek, 1971, 1975; Velásquez, 1972) to local areas where the species are eaten fresh or prepared as salad vegetable, pickled or even preserved by smoke-drying. In China, G. divaricatum is additionally used for treatment of stomach ailments, hemorrhoids and fistula (Tseng and Chang, 1984). No quantitative estimates exist in the literature of the amounts consumed as food in these different areas.

Several species of Gelidium and Pterocladia have been traditionally used in Japan, China and Korea for making jellies which are consumed together with other types of food. In the past century, P. lucida was also used in this way in Western Australia (Michanek, 1975).

9.3 and 9.4 Animal Fodder and Manure

No information concerning the utilizatin of species of Gelidium or Pterocladia as animal fodder or fertilizer was found. The nearest information is the one reported by Li and Chiang (1983) using G. cartilagineum as plastic agent in the artificial diet of the silk worm, Bombyx mori.

9.5 Industrial Products and Processes

Species of Gelidium and Pterocladia are among the most important agarophytes in the world. they constitute about 40-50% of the world's annual use of agarophytes, estimated at about 39 000 t of dry matter (whyte and Englar, 1981). About 35 species are harvested throughout the world (Table 4) as raw materials for the 6 500-7 000 t of agar produced annually (Yaphe, 1959; Stoloff and Silva, 1957; Levring, Hoppe and Schmid, 1969; Yamada, 1976). The leading agar producers are, according to Yamada (1976), Japan with an annual production of 2 300 t of agar followed by Denmark with 1 200 t, and Spain with 800 t. However, Michanek (1975) has reported Portugal as the

second-most important producer with 6 factories in operation and capacity for annual production of 1 620 t of agar. Other agar-producing factories are in Chile, Mexico, the USA, New Zealand, South Korea, India, France and Morocco.

The agar content of several species of Gelidium and Pterocladia has been studied and the values of twelve of them are summarized in Table 6. Yields and quality of agar vary with species of algae, karyological phase of the plant, nitrogen content of the thallus, season, location and environment (see references in Table 6). Commercially, 17-25% yields from agarophytes are considered normal (Whyte and Englar, 1981). However, agar concentration found in several species can be far above this value. Thus, the agar content of Gelidium robustum from California can be as high as 70% (Levring, Hoppe and Schmid, 1969). The values recorded in this species are a good example of the habitat and locality-related variation possible in agar content of these species. In the intertidal

Table 6

Agar content of several species of Gelidium and Pterocladia on a dry weight basis

Species	Locality	Fishing area number	Amount of agar	References
Gelidium amansii	Japan	61	25 to 30%	Levring, Hoppe and Schmid, 1969
Gelidium chilense (= filicinum)	Chile	87	25 to 31%	Santelices, Oliger and Montalva, 1981
Gelidium latifolium	Java	71	25 to 35%	Levring, Hoppe and Schmid, 1969
Gelidium lingulatum	Chile	87	20 to 24%	Santelices, Oliger and Montalva, 1981
Gelidium micropterum	India	51	43%	Levring, Hoppe and Schmid, 1969
Gelidium pristoides	South Africa	34	30 to 48%	Carter and Anderson, 1986
Gelidium pusillum	Philippines	71	41%	De León and Domantes,1974
	India	51	50%	Kaliaperumal and Umumaheswara Rao, 1981
Gelidium purpurascens	California, USA	77	25.4%	Whyte and Englar, 1981
Gelidium robustum (= cartilagineum)	California, USA	77	40 to 45%	Barilotti and Silverthorne, 1972
Gelidium sesquipedale	Portugal	27	24%	Da Fonseca, 1966
Gelidium spinolosum	Morocco	34	33%	Levring, Hoppe and Schmid, 1969
Gelidium sp.	Sri Lanka	51	21 to 40%	Arumugam, Sivapalan and Theivendirarajah, 1981
Pterocladia capillacea	North Africa		25%	Levring, Hoppe and Schmid, 1969
	Turkish coast	37	10 to 15%	Güven and Güler, 1979
Pterocladia heteroplastos	India	51	35%	Kaliaperumal and Umumaheswara Rao, 1981

populations, the maximum agar production was (Cooper and Johnstone, 1944) in June and the minimum in February, probably in correlation with the shorter days, lower temperatures, higher and rougher surf and greater cloudiness occurring from January to March. In subtidal populations the peak production occurred (Barilotti and Silverthorne, 1972) from September to November and it was related to increasing temperatures. Likewise, in G. amansii from Japan there was (Boney, 1965) a steady increase in agar content through the summer and winter, reaching a maximum in autumn and then falling again. For both G. amansii and G. robustum, Boney (1965), and Barilotti and Silverthorne (1972) have recommended harvesting at the time of maximum agar content.

Traditionally, separation of agar has yielded two fractions (Izumi, 1971). One fraction was rich in neutral components and the other rich in acidic elements. The former was named agarose and shown to be a linear, nearly homogeneous molecule composed of alternating residues of D-galactopyranose and 3,6 anhydro L-galactopyranose. The latter fraction, named agaropectin, was assumed to be homogeneous and shown to have pyruvic acid bonded to D-galactopyranose residues. Later studies, however (Duckworth and Yaphe, 1971; Fuse and Goto, 1971; Izumi, 1971) have shown that the concept that agar is made up of two polysaccharides (neutral agarose and charged agaropectin) is an over-simplification. Agar is a complex mixture of polysaccharides having the same backbone structure but substituted to a variable degree with charged groups. More recently, Friedlander, Lipkin and Yaphe, (1981), have suggested that the high gel strength and the isothermal gelling temperatures of P. capillacea from the Israeli Mediterranean coast may be related to a low sulphate content and low molar ratio of galactose to 3.6 anhydrogalactose.

In recent years, agarose has been rapidly replacing traditionally used agar in biomedical applications because of the relative absence of anionic constituents in it as compared with agar. In fact, agarose superiority over agar for biomedical usage extends (Renn and Mueller, 1967) to electrophoresis, immunology, microbiology and gel diffusion chromatography, and it is predicted that it will continue replacing agar as its advantages become further known, and as demand dictates increased production, better uniformity and lower prices. Since agarose is purified from high quality agar, utilization of species of Gelidium and Pterocladia is likely to keep increasing in the future.

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